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Energetics and Nutrition of British and Icelandic Redshank (*Tringa totanus*) During the Non-breeding Season

by

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Abstract

Energetics and Nutrition of British and Icelandic Redshank (*Tringa totanus*) During the Non-breeding Season

Paul Ian Mitchell

Prolonged severe winter weather increases mortality in shorebirds wintering in Britain, with Redshank suffering much more than other species. I studied eco-physiological factors which might affect the chances of survival of Redshank to determine whether British-breeding Redshank (*T. t. totanus*) and the larger Icelandic-breeding Redshank (*T. t. robusta*) are equally affected.

I examined the seasonal changes in body mass (BM), total lean mass (TLM) and mass of fat (FM) in wild and captive birds of both races in NE England, using total body electrical conductivity. I measured mass-specific standard metabolic rates in both races at temperatures (T_a) between -5°C and 25°C using open-flow respirometry. By combining these with measurements of heat loss from heated taxidermic mounts of Redshank, I calculated the effects of air temperature, wind speed and solar radiation on maintenance metabolism (M_{maint}) of each race. I also measured the composition of carcasses of Redshank which died on the Wash, SE England following prolonged severe weather in February 1991.

I found that i) both races accumulated similar fat reserves during mid-winter as an insurance against impending bad weather and food shortages; ii) *robusta* had a higher mass-specific basal metabolic rate (BMR) and higher thermal conductivity (K_{es}); iii) severe weather mortality in Redshank in Britain coincided with time periods when M_{maint} in both races exceeded 2.5xBMR and daily mean temperatures were -2°C or below continuously over a period of 5 days; iv) there were no racial differences in foraging behaviour; v) both races died during severe weather as a result of starvation after depleting almost all fat and similar amounts of protein reserves; vi) the reserves of *robusta* would sustain them without food for 0.5 days less than *britannica* exposed to the same weather conditions.

The differences in BMR between the two races was discussed in terms of differences in breeding latitude and migratory lifestyle. The higher K_{es} of *robusta* was thought to result from the higher BMR, rather than a lower level of insulation provided by the plumage. During severe weather when food availability is reduced, I would predict that *robusta,* with their higher mass-specific M_{maint} and larger body size, would find it more difficult to meet their daily energy requirements through food intake alone. Given that the energy obtained by *robusta* from fat and protein reserves would sustain them for shorter periods than those of *britannica*, I would predict that during periods of prolonged severe weather, the latter would have a greater chance of survival.

No part of this thesis has previously been submitted for a degree in this or any other university. The work described is my own except where duly acknowledged.

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3.0 **Energy Expenditure**

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This research would not have been possible without the constant support (both spiritual and financial) and encouragement from my parents Barbara and Alan, and my brother Stephen whose reference to facial hair has inspired not only myself, but also close friends, to better things. Thankyou to Sarah for her remarkable patience and tolerance throughout the highs and lows of the past two years.

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For my parents and family

For the memory of

Frederick Mitchell (1905 - 1987)

Agnes Mitchell (1907 - 1976)

Harold Hill (1910 - 1981)

Marjorie Hill (1915 - 1996)

Joseph Morris (1911 - 1995)

"Do not go gentle into that good night.

Rage, rage against the dying of the light."

- Dylan Thomas

1.0 Introduction

*"On February 15th, during a short visit to the beach at Lowestoft, I found a Redshank (*Tringa totanus*) which had evidently sought shelter under the lee of a marram-tufted sand hill. During the night the snow had formed a drift around it, so that only it's head was visible. It was frozen stiff in an attitude of sleep."*

- F. C. Cook (1929); in: Witherby & Jourdain (1929).

1.1 Overview

This thesis is concerned with the factors which may affect the mortality of two races of Redshank which breed in Iceland and northern Britain respectively, whilst spending the non-breeding season together at Teesmouth in north-east England. It investigates the energetic demands imposed on the two races and their ability to meet them during prolonged severe winter weather which inflicts the highest rate of mortality during the annual cycle of Redshank. In doing so, it considers the implications of differences between the races in breeding origin, body size and behaviour on their energetics, nutrition and ultimately, survival.

1.2 Severe weather mortality in Redshank and other shorebirds

During their annual cycle, most shorebirds wintering in mid-northern latitudes experience a higher rate of mortality on the non-breeding grounds than on the breeding grounds or during migration (Evans, 1991). Mortality of birds due to severe winter weather has been documented many times during the twentieth century since the severe winter of 1916/17 (Jourdain & Witherby 1918a&b). However, accounts of this and other severe winters during the first half of the century (1928/29: Witherby & Jourdain, 1929; 1939/40: Ticehurst, Witherby & Hawke, 1940; 1946/47: Ticehurst & Hartley, 1948) were based on isolated observations and anecdotal evidence from individuals such as F. C. Cook in Lowestoft, Suffolk in 1929 (see quotation above). Hence, although it was evident that large numbers of birds died in some places during severe weather, there was no clear information on the extent of the mortality on a national scale, of the overall effect on population size and age structure, and on which species were most vulnerable. Following the severe winter of 1962/63, the coldest on record since 1750, co-ordinated collection of information from British ornithologists improved greatly (Dobinson & Richards, 1964). During previous winters it was not clear whether the large numbers of carcasses being found during severe weather were merely results of more intense searches and greater awareness from observers. During the winter of 1962/63, however, several studies showed an increase in mortality rate, determined from counts and recoveries of dead ringed birds, compared to previous years (e.g. Boyd & Ogilvie, 1964; Beer & Boyd, 1964; Beer, 1964).

During the winters of 1982/83 - 1985/86 the Wader Study Group investigated the effect of severe weather on shorebird survival on British estuaries and ensured that constant search effort for carcasses was maintained throughout (Davidson & Clark, 1982). The results of the study clearly demonstrated that winter mortality in shorebirds increased as a result of severe weather; for instance, along 86km of coastline, over 500 corpses were found during each of the severe winters of 1984/85 and 1985/86, compared to only 62 and 128 during the milder winters of 1982/83 and 1983/84 respectively (Davidson & Clark, 1982, 1983a&b,1984, 1985a&b; Clark & Davidson, 1986). The study also showed that some species were more susceptible to severe weather than others. Redshank made up 49% of the total numbers of corpses recovered in 1984/85, Dunlin (*Calidris* alba) 15% and Oystercatcher (*Haematopus* ostralegus) 11%. Redshank also predominated among the corpses found in 1985/86, making up 55%, although in both years the species formed a much smaller percentage (ca. 5%) of the total numbers of shorebirds at risk (Cranswick *et al.*, 1995). Studies conducted during other years have also found Redshank to predominate amongst the corpses found during severe weather; for example, they constituted 52 % of shorebird and 24% of all waterfowl corpses found on The Wash, East Anglia, in 1962/63 (Pilcher, 1964) and 51% of a total of 4,825 shorebird corpses found in south-east England in 1990/91 (Clark *et al.*, 1993). Redshank are therefore clearly likely to suffer heavier additional mortality as a result of severe winter weather than any other shorebird species.

Severe weather events can have a very dramatic effect on Redshank numbers wintering in a certain area. For instance, the 1,553 Redshank corpses recovered on The Wash in 1991(an underestimate of the actual number which died since some corpses will have been washed out to sea) represented 40% of a mean of 3,900 present on the Wash in February during the previous 4 years. Immediately afterwards, in March 1991, only 880 Redshank remained on the Wash, just 26% of a mean of 3,328 for March in the previous years (Clark *et al.*, 1993). Although it is likely that some birds moved away from the area during the severe weather (Baillie, 1984), the numbers that had been killed in 1991 had a noticeable effect in the subsequent winter when all monthly maximum counts of Redshank were below mean monthly maxima for 1987-90. In addition, a greater proportion of first year birds wintered on the Wash in the winter of 1991/92, perhaps the result of a decrease in competition on the feeding grounds due to a much reduced wintering adult population, rather than from a sharp increase in breeding productivity in the summer of 1991 (Clark *et al.*, 1993).

It is unclear why Redshank suffer greater losses in severe weather than other species wintering in the same areas. It is also unclear whether certain categories of Redshank are more susceptible than others. Some studies have attempted to investigate the presence of any sexual bias in Redshank mortality during severe weather (Davidson & Clark, 1985b; Clark *et al.*, 1993), though lack of information on sex ratios in populations prior to the onset of severe weather have made such studies inconclusive. (The sex of Redshank can be determined only by gonad inspection outside the nesting season (Prater *et al.*, 1977)). No studies have investigated whether Redshank from British and Icelandic breeding populations (see below), both of which over-winter in Britain, are equally affected during severe weather.

1.3 Breeding origins of Redshank wintering in Britain.

Hale (1971) identified 3 races of Redshank in Europe; *Tringa totanus totanus* which breeds in mainland Europe, an Icelandic race *T. totanus robusta* and the British breeding population *T. totanus britannica.* There are sufficient biometric differences between *robusta* and *totanus*, the latter being smaller in body size, for these two races to be considered as subspecies, whereas *britannica* shows considerable overlap in biometry and is considered in evolutionary terms, to be a hybrid of the two sub-species. However, *robusta* does have significantly longer wings, tarsus-toe length and smaller bill length than *britannica* and can be distinguished on measurements using discriminant function analysis (Summers *et al.*, 1988).

Hale (1973) used biometrics, actual ringing recoveries and computer-predicted ringing recoveries to determine the winter ranges of different breeding populations of Redshank from around the world. *T. t. robusta* winter chiefly in UK, Ireland, Netherlands, Denmark and Iceland; *britannica* move on average, no more than 300km during the non-breeding season (Hale, 1973) and so tend to be restricted in winter to the UK where very few of the European subspecies *totanus* occur. However, small numbers of *britannica* do venture to the Netherlands, northern

France and the north Iberian coast. These may be first-year birds which tend to move greater distances than adults during the winter (Hale, 1973). The British wintering population thus comprises *robusta* and *britannica* on the east and west coast whilst the south coast tends to be dominated by *britannica* (Furness & Baillie, 1981).

A sample of around 1500 Redshank which died following severe weather on the Wash in 1991 contained proportionately more birds with longer wings than samples of birds present at the same time in previous winters (Clark *et al.*, 1993). It is not clear, however, whether this apparent bias in casualties in 1991 indicates a greater susceptibility of *robusta* to severe weather than of *britannica*. However, this does raise the question of differential survival during severe winter conditions between these two races of Redshank, since differences in body size, breeding latitude and behaviour could lead to differences in energetic, nutritional and behavioural factors which contribute to survival during severe weather and the non-breeding season as a whole.

1.4 Factors affecting survival of British and Icelandic Redshank during severe weather.

1.4.1 Storage of Fat and Protein

The primary form of energy storage in birds is lipid in the form of triglycerides (Blem, 1976). Fat is stored in discrete depots subcutaneously and associated with the mesenteries and, for more immediate use, intercellularly in muscles and the liver. King & Murphy (1985) make the distinction between nutrient stores and nutrient reserves. Stores are not accumulated for immediate metabolic needs, but in anticipation of future nutritional stress which they define as when .."*an animal's nutrient demands exceeds its nutrient ingestion, resulting in net catabolism in body tissues to the extent that one or more vital physiological functions are impaired*". Nutrient reserves include those compunds which are stored plus any other tissues which are not primarily accumulated to insure against future nutritional stress, but can be catabolised to *"forestall stress"*.

Most species of shorebird exhibit marked seasonal variations in body mass attributable to the accumulation and utilisation of fat and to a lesser extent, protein reserves (Scott *et al.*, 1994). The greatest accumulation of nutrient reserves occur in shorebird species which breed at high northern latitudes but migrate to lower latitudes during the non-breeding season. Up to one third of the body mass of long distance migrants such as Knot (*Calidris canutus*), Sanderling (*C. alba*) and Dunlin is composed of lipid reserves to fuel flight (Gudmundsson *et al.*, 1990; Davidson & Evans, 1989). Premigratory increases in pectoral muscle protein also occur, not only to provide increased flight power (Marsh, 1984) but also as protein stores to buffer food shortages on the breeding grounds or to accelerate egg production (Davidson & Evans, 1990).

Shorebirds wintering in mid-northern latitudes show substantial body mass increases in mid-winter (for review see: Scott *et al.*, 1994; for examples see: Davidson, 1981a; Johnson, 1985, Scott, 1991). These mid-winter weight increases appear to be solely attributable to the accumulation of fat stores, with no hypertrophy of flight muscles taking place (Evans & Smith, 1975; Davidson, 1981; Scott, 1991). The greater the accumulation of fat stores, the longer a shorebird will be able to survive when energy intake from food is exceeded by energy output during prolonged periods of poor feeding or severe weather. The larger Icelandic Redshank *robusta* may be able to carry a greater mass of fat than the smaller *britannica*. However, both races do not maximise the amount of fat they carry in mid-winter, since winter levels are always exceeded during premigratory fattening (Scott *et al.*, 1994).

Lima (1986) suggested that birds optimise their body mass in winter in response to trade-off between i) accumulating sufficient fat reserves for sustenance during periods of negative energy balance, and ii) incurring costs associated with being heavy (Witter & Cuthill, 1993), in particular the increased risk of predation (Gosler *et al.*, 1995). If so, fat should be accumulated to reach a peak when the chance of encountering a negative energy balance due to severe weather is greatest. Levels should then be allowed to fall as the chance of severe weather decreases. Evidence for such a seasonal regulation of body mass according to Lima's optimisation model has been found in passerines (Evans, 1969; Rogers, 1987, 1995) and in some shorebirds (Pienkowski, 1979; Davidson, 1982a). However, some authors attribute the observed mid-winter accumulation of fat and subsequent depletion to a change from good feeding conditions in autumn to poorer feeding accompanied by higher thermogenic demands as winter progresses (Maron & Myers, 1985; Owen & Cook, 1977).

Davidson (1982a) concluded that, unlike other shorebird species Redshank wintering along the east coast of Britain were unable to regulate mid-winter body mass or prevent its subsequent decline in late winter. Davidson suggested that cold autumn and early winter weather in eastern Britain reduced food availability to a point where Redshank were unable to ingest enough food to both meet immediate energy demands and to accumulate fat stores which would insure against future negative energy balances. Some studies (Beecroft & Clark, 1985; Norman & Coffey, 1994; Scott, 1991; Scott *et al.*, 1994; Swann & Etheridge, 1989) have presented evidence which questions Davidson's conclusions.

Though Scott (1991) presents some data on monthly body masses of the two races, no study has fully documented how body mass and fat and protein reserves in *robusta* and *britannica* vary during the winter or investigated whether these are maintained at internally regulated levels, or vary according to feeding conditions. It might be expected that the smaller *britannica* would require a lower food intake to meet its daily energy requirements than the larger *robusta,* but the respective abilities of the two races to maintain a positive energy balance and accumulate fat reserves before mid-winter are highly dependant on the levels of energy expended by the two races under the same weather conditions (see below).

The amount of time which both races could survive a sustained negative energy balance by using energy from reserves is largely dependant on the size of fat and to a lesser extent, protein reserves and the rate of energy expenditure. The rate at which energy is expended affects survival time by determining the rate at which reserves are used up. Higher rates of energy expenditure require larger masses of lean metabolically active tissue to sustain them and birds die when the mass of lean tissue is no longer large enough to produce the required energy output. Hence, birds die with larger lean masses following periods of higher energy expenditure (Piersma *et al.,* In Press). Small shorebird species such as Dunlin and Turnstone (*Arenaria interpres*) which have higher mass-specfic metabolic rates than larger species, die with proportionately larger fat and protein reserves remaining (Clark & Davidson, 1986). This may result from an inability to mobilise reserves fast enough to meet immediate energy requirements, hence hypothermia sets in whilst reserves remain unused (Davidson & Evans, 1982; Swennen & Duiven, 1985).

Therefore, in order to compare potential survival times of *robusta* and *britannica,* it is important to consider not only the levels of fat and protein reserves, or the rate of energy expenditure of both races, but the proportion of these reserves that are used up prior to death.

1.4.2 Rate of Energy Expenditure

It is reasonable to expect differences between the two races in the rate of energy expended under the same thermal conditions and activity regimes, because of known effects of body size, breeding latitude and migratory behaviour on the energy expenditure of birds. Firstly, basal metabolic rate (BMR) increases allometrically with body mass (Aschoff & Pohl, 1970; Lasiewski & Dawson, 1967; Kendeigh *et al.*, 1977; Gavrilov & Dolnik, 1985), though shorebirds have a higher BMR for a given body mass than other non-passerines (Castro, 1987; Kersten & Piersma, 1987; Scott, 1991). Thermal conductance, a measure of the rate of heat loss, also increases allometrically with body size (Turner, 1988). Therefore, due to a larger body size and its effect on BMR and thermal conductivity, *robusta* would be expected to have a greater total energy expenditure to maintain body temperature under the same thermal conditions as *britannica.*

Total energy expenditure is not just a consequence of body size. The metabolic output per unit mass of tissue (mass-specific BMR) may vary between races as a result of differences in migratory behaviour and breeding latitude. Kersten & Piersma (1987) explained the higher mass-specific BMR of shorebirds in general, compared to other non-passerines, as an adaptation to an energetically expensive way of life (the 'Energetic Margin' hypothesis). They argued that a high mass-specific energy output from the tissues of shorebirds would enhance their capabilities to meet the energetic demands of long-distance migration or prolonged severe weather on temperate wintering grounds. The Energetic Margin Hypothesis may be applicable to the comparison between the two races; in that *robusta* is migratory (flying about 1700km between Iceland and Eastern England), whilst *britannica* is almost non-migratory.

Kendeigh & Blem (1974) and Kendeigh (1976) found that the existence metabolism (under standard conditions) of the North American House Sparrow (*Passer domesticus*) increased with increasing latitude of residence (between 9°N and 59°N) and hence, colder climate. Weathers (1979) also found a latitudinal cline in avian mass-specific BMR, increasing in species resident at higher latitudes; possibly an adaptation to higher energy requirements for maintenance in the colder climates at higher latitudes.

Icelandic Redshank *T. t. robusta* breed between 63°20'N and 66°30'N (also at 62°N on the Faroe Islands) further north than the breeding range of *britannica*, between 50°N and 58°36'N on the British mainland and at 60°50'N in the Shetland Isles. This latitudinal difference may be sufficient for *robusta* to have evolved a higher mass-specific BMR than the more southerly breeding *britannica* (cf. Weathers, 1979). This of course depends on how strong the selective pressures are on the breeding grounds as compared to the non-breeding grounds. In terms of variation in body size and plumage characteristics in Redshank worldwide, Hale (1971) argues that the strongest correlations exist with the breeding origin, whereas Salmonsen (1954) concluded that, in light of the migration patterns throughout the range of the Redshank in Eurasia, conditions on the non-breeding grounds exert the higher selective pressures.

1.4.3 Food Intake

During severe winter weather the chance of encountering a negative energy balance increases not only because energy demands for thermoregulation increase (see above), but because a reduction in prey availability may occur and result in a lower rate of intake of energy from food (e.g. Evans, 1976; Dugan *et al.*, 1981; Pienkowski *et al.*, 1984). It appears that *robusta* may be expected to have higher overall energy demands than *britannica* at least because of their larger body size (see above), and would therefore, need to obtain more food per day. As a consequence, *robusta* may be less able to balance their energy budget through feeding during severe weather or have less excess energy from food which to convert into nutritional stores. Hence, the ability to meet energy demands through feeding at a particular time could have not only immediate survival implications, but also longer term consequences by affecting the ability to accumulate sufficient 'insurance' of fat and protein.

1.5 Study Area and Wintering Redshank Population

The Tees Estuary or Teesmouth (54°37'N 1°12'W) in north-east England holds large numbers of shorebirds and wildfowl over winter and during spring and autumn migrations. The largest inter-tidal area in the estuary is Seal Sands (Figure 1.1) which comprises 140 hectares of sand and mud. Seal Sands is included in the area which was designated as a National Nature Reserve by English Nature in 1995 under the Wildlife and Countryside Act (1981).

Teesmouth is nationally important for Redshank, in that it regularly supports more than 1% of the population wintering in Britain. Numbers are highest in autumn, peaking in August and September when the Redshank are undergoing feather moult. Numbers then decline and reach their lowest during mid-winter before increasing sharply in March and April (Figure 1.2) before most Redshank leave for their breeding grounds. Biometrics of Redshank wintering at Teesmouth indicate both Icelandic and British breeding to be present (see Chapt. 2). This is confirmed by ringing recoveries (summarised by R. M. Ward & P. R. Evans, unpubl.) which show Teesmouth Redshank to originate from breeding grounds throughout Iceland and the eastern half of northern Britain. Both *robusta* and *britannica* start to arrive in July (1 recovery each) and commence moult at the same time (Mitchell *et al.*, 1996), contrary to previous suggestions that *robusta* moults later than *britannica* (Furness & Baillie, 1981). Redshank complete moult before the majority leave Teesmouth in late Autumn (Mitchell *et al.*, 1996). Few birds have been recovered outside the area during winter which suggests that birds disperse inland or along the coast locally. Recoveries generally indicate high site fidelity between years, in adults at least. Recoveries of juveniles ringed at Teesmouth in autumn indicate a widespread multi-directional dispersal similar to that shown by Hale (1973). There are also a few recoveries of adults during spring when numbers at Teesmouth increase once more, suggesting the return of

Figure 1.1: The position of Seal Sands and other inter-tidal areas around the Tees estuary (Teesmouth).

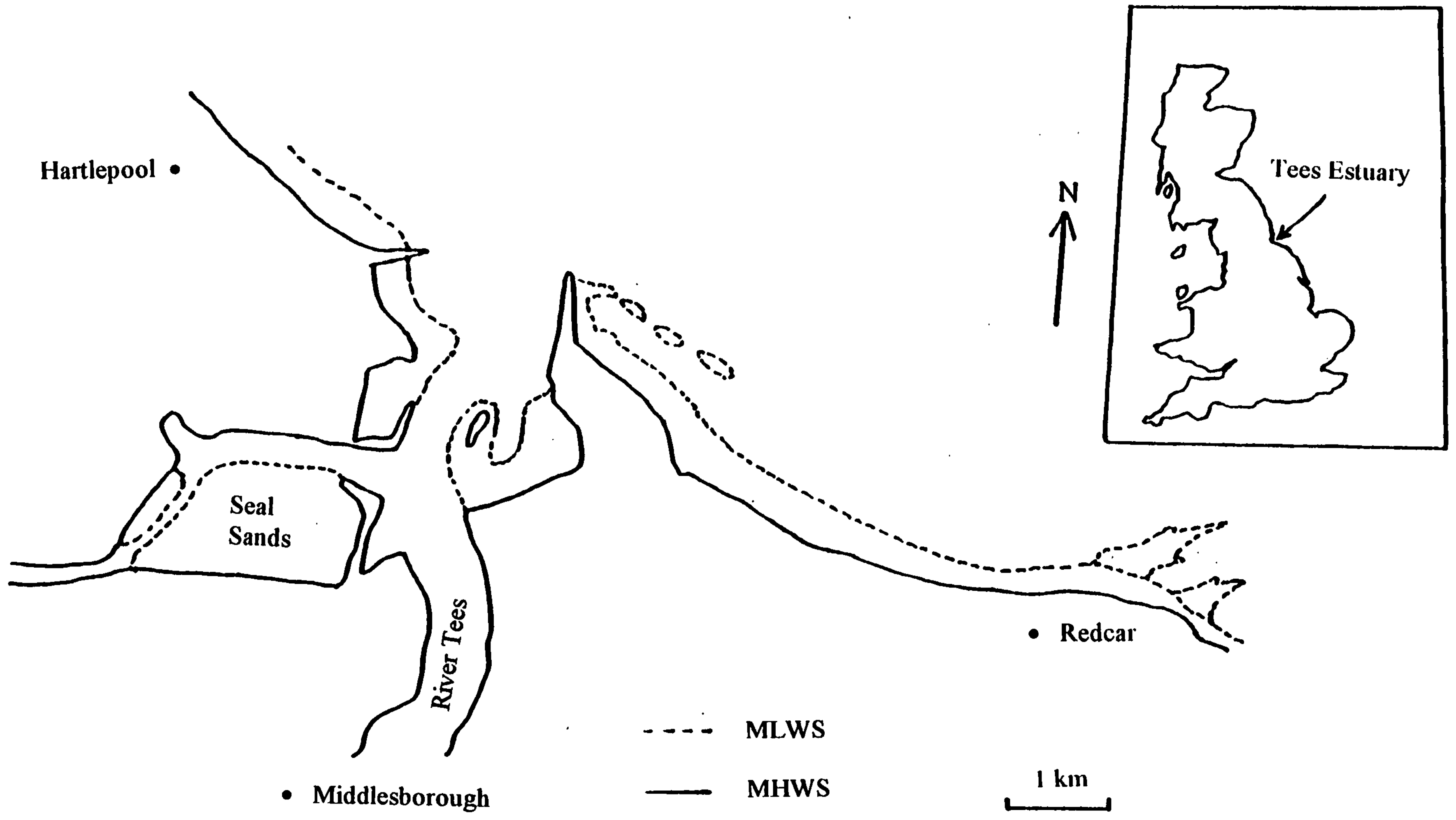
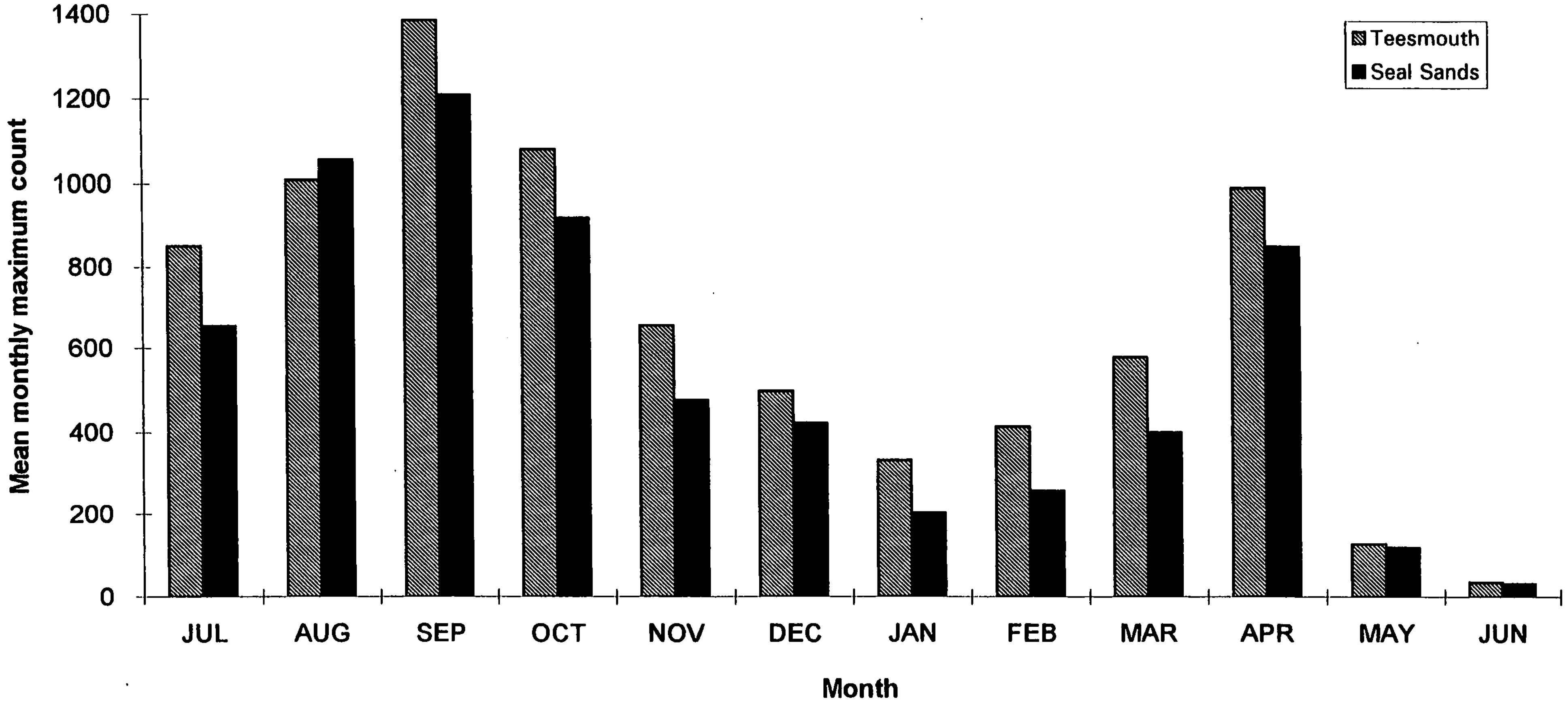


Figure 1.2: Mean monthly maximum low-water counts (1990-95) of Redshank at Seal Sands and Teesmouth.



locally wintering birds, though some spring birds do originate from the Wash (3 ringed in Autumn) and Cheshire (1 winter recovery).

1.6 Organisation of the thesis

Chapter 2 presents changes in body mass and body composition of the two races during the non-breeding season. It also investigates whether body mass changes are internally regulated or are determined by food supply.

Chapter 3 combines measurements of BMR and thermal conductivity of the two races with measurements of heat loss from heated taxidermic mounts to estimate and compare between races, the levels of energy expended for maintenance metabolism (M_{maint}) under different weather conditions. M_{maint} was then estimated for previous winters when severe weather had caused large-scale mortality in Redshank, in order to determine under what weather conditions Redshank are most likely to die.

Chapter 4 compares the foraging behaviour of both races, to investigate their abilities to meet their respective energy demands through feeding under different weather conditions.

Chapter 5 examines the extent of catabolism of fat and protein reserves in both races prior to death during severe weather. Survival times were estimated for each race by incorporating information on rates of energy expenditure and the levels of fat and protein available for assimilation into energy.

Finally, **Chapter 6** presents a general discussion on i) whether mortality would be expected to be higher in one race than the other, given the evidence presented in chapters 2 to 5; and on ii) probable causes of the higher mortality in Redshank during severe weather compared to other shorebird species.

2.0 Seasonal Changes in Body Mass and Body Composition of Icelandic (*T. t. robusta*) and British Redshank (*T. t. britannica*)

2.1 Introduction

This chapter describes quantitative changes in body mass during the non-breeding season in wild and captive individuals of the two races of Redshank wintering at Teesmouth. The main aim of this study was to determine whether the nutritional preparation for winter in terms of the accumulation of fat and protein stores is similar in both races of Redshank.

Severe winter weather conditions in northern latitudes can reduce food availability, sometimes to zero, and, combined with increased energy demands for thermoregulation and foraging, create a deficit in the energy budget of a homoeotherm. The ability of an animal to survive periods during which energy intake from food is less than its energy requirements is positively correlated with its fat reserve (Dugan *et al.*, 1981; Le Maho *et al*, 1981; Cherel *et al.*, 1987). It has been suggested that shorebirds can regulate their body mass seasonally at optimal levels in accordance with seasonal variations in weather and food supply (Pienkowski *et al.*, 1979; Swann & Etheridge, 1989; Scott *et al.*, 1994) but that Redshank wintering on the east coast of Britain are unable to regulate their body mass (Davidson, 1982a). This chapter considers whether, in spite of Davidson's claim, Redshank at Teesmouth in NE England are capable of regulating body mass, by comparing the seasonal body mass changes of captive Redshank with those in the wild.

It was described in Section 1.4.1 how shorebirds wintering in Britain and other northern temperate regions exhibit a seasonal pattern of change in fat levels and body mass. Fat stores are laid down between arriving on the wintering grounds and late December. This is followed by a relatively rapid decline in fat levels until the end of February, then by a pre-migratory increase in March, April or May depending on species and timing of migration. Redshank over-wintering in Britain appear to accumulate smaller fat stores in mid-winter than other species and also lose mass at a faster rate during February and March (Davidson, 1981a). It is unclear whether both races exhibit the same pattern of body mass change since there are no studies on seasonal body mass change in Redshank which have distinguished between *robusta* and *britannica.*

Since *robusta* are significantly larger in body size (Hale, 1971; Summers *et al.*, 1988) and are consistently heavier than *britannica* (Scott, 1991), the overall seasonal changes in body mass reported for Redshank (e.g. Davidson, 1982a; Johnson, 1985) could be greatly affected by changes in the relative proportions of the two races in a population at any given time. No data were available on changes in race ratio throughout the winter in previous studies.

Evidence for the internal regulation of body mass in shorebirds is based on correlations of body mass with ambient temperature, in that heavier birds are found at sites with lower winter temperatures and therefore greater thermogenic costs and possibly lower food availability (Davidson, 1982a; Pienkowski *et al.*, 1979; Scott, 1991). Davidson concluded that low mid-winter temperatures prevented Redshank on the east coast of Britain from accumulating sufficient fat to insure against subsequent severe weather. Swann & Etheridge (1989) showed, however, that during December and January mean body masses of Redshank, Knot and Oystercatcher on the Moray Firth, Scotland, were higher at lower ambient temperatures. Such evidence indicates a proximate response to temperature at a given time (Rogers, 1995) and not necessarily a pre-programmed ultimate response to predicted seasonal changes in ambient temperature as modelled by Lima (1986) and first demonstrated in Yellowhammers (*Emberiza citrinella*) by Evans (1969). Various studies (Beecroft & Clark, 1986; Davidson, 1981; Davidson & Clark, 1985b; Norman & Coffey, 1994; Pienkowski *et al*, 1979) show additional evidence for a proximate regulation of body mass by demonstrating that shorebirds (including Redshank) which have sustained large losses in body mass during prolonged severe weather can recover such losses when conditions improve. Body mass gains following severe weather have occurred in Redshank during January and February (Beecroft & Clark, 1986; Norman & Coffey, 1994), the time when Davidson (1982a) had suggested that body mass could not be regulated. However, all observations of weight gain following severe weather have been based on the mean body mass of populations. This may increase following the selective death or emigration of lighter birds and not represent an increase in body mass of individuals.

In order to determine directly whether east coast Redshank are capable of regulating body mass in an ultimate sense, I will compare seasonal changes in body mass of wild Redshank at Teesmouth with those of Redshank in captivity. Scott (1991) suggested that if captive birds were given food *ad libitum* throughout the winter and experienced less harsh weather conditions, any significant seasonal changes in body mass should be due to internal regulation rather than external regulation by the environment. If the seasonal nutritional changes of wild birds were to mirror those of captive birds, then they too must be capable of internally regulating body mass. Conversely, if Redshank are prevented by environmental constraints from maintaining body mass in the wild, captive birds should be heavier than their wild conspecifics and not show a reduction in body mass during the second half of winter. Scott (1991) found that body mass of captive Redshank declined more slowly during January and February than in wild Redshank at

Teesmouth, leading to the conclusion that east-coast Redshank could not internally regulate body mass. However, the four Redshank in Scott's study were held only between November and February and not through to March when the body mass of Redshank on the east-coast of Britain falls to its lowest levels (Davidson, 1981a & 1982a; Johnson, 1985; Scott, 1991), hence an incomplete pattern of seasonal body mass change was presented by Scott.

Whilst most studies (Pienkowski *et al.*, 1979; Davidson, 1982a) have assumed that body mass changes in shorebirds during winter result from changes only in fat stores, Davidson *et al.* (1986) demonstrated that protein is also stored and regulated, proximately at least. This raises the question of whether protein stores and fat stores are regulated separately at independently set levels, or whether overall body mass is being regulated. The way in which protein and lipid stores are controlled to regulate body mass will be investigated in this study by comparing the levels of lipids and lean tissues of wild birds with those brought into captivity.

In Appendix II, I develop and test existing predictive formulae of Scott *et al.* (1991) and Scott *et al.* (1994) utilising TOBEC to estimate total lean mass (TLM), and hence lipid mass in Redshank. In my study TOBEC was employed to measure seasonal changes in TLM and lipid stores in both races of Redshank at Teesmouth.

2.2 Methods

2.2.1 Seasonal changes in body mass

A total of 1,867 Redshank were caught by cannon-net and mist-net at Teesmouth between 1983 and 1995 and weighed to the nearest gram using a Pesola spring balance. Age was determined from plumage characteristics (Prater *et al.*, 1977) with birds being identified as less than 1 year old (i.e. first years, Euring codes 3 and 5) and greater than 1 year old (i.e. adults, Euring codes 4 and 6). Measurements of wing-length (maximum chord) and tarsus-toe (tibiotarsus-tarsometatarsus joint to end of flesh on longest digit) were taken to the nearest millimeter using a stopped rule and of bill-length to the nearest 0.1mm using vernier callipers. All four biometrics were taken on a total of 633 adults. The discriminant function of Summers *et al.* (1988) which incorporates wing-length, bill-length and tarsus-toe was used to assign each bird to a race. The discriminant function assigns a probability P to an individual Redshank being *robusta.* Birds were assigned as *robusta* if $P \geq 0.7$, and *britannica* if $P \leq 0.3$. If $0.7 > P > 0.3$, no race was assigned. This was a sufficient buffer to substantially reduce the chance of mis-identification resulting from variation in accuracy of measurement between observers (see Appendix I). A large majority of the measurements were taken by one person (R. M. Ward) which minimised the variability in accuracy of measurement and thus further reduced the chance of mis-identification (Appendix I). Furthermore, the discrimant function did not appear to introduce any sexual bias into the sample of Redshank whose race was predicted with a probability of greater than 0.7 (Appendix I).

2.2.2 Size-adjustment of body mass

The body mass of each individual was adjusted for body size in order i) to control the mean body mass of the Teesmouth population for changes in the proportions of *britannica* and *robusta* and ii) to control for body size differences when comparing body mass between the two races. Univariate biometrics are poor measures of overall body size in birds (Freeman & Jackson, 1990), therefore principal component analysis (PCA) was conducted on wing-length, bill-length and tarsus-toe to produce a single 'body-size' factor (Rising & Sommers, 1989; Freeman & Jackson, 1990; Bolton *et al.*, 1991). Only one factor was extracted by the PCA with loadings of 0.71 for wing-length, 0.74 for bill-length and 0.78 for tarsus-toe. The model for the size factor is given in equation 2.1.

$$S = (0.501 * wl) + (0.543 * bl) + (0.614 * tt) \qquad \textbf{2.1}$$

where S = body size, wl = wing-length, bl = bill-length, tt = tarsus-toe.

S calculated for each individual was subtracted from the mean size factor (S') of the 633 adults measured at Teesmouth between 1983/84-1994/95 to give an index of deviation in size S_d. (equation 2.2).

$$S_d = S' - S \qquad \textbf{2.2}$$

where $S' = 160.5$.

Body mass was regressed against S for the 633 adults caught at Teesmouth

(1983/84-1994/95) (equation 2.3).

$$BM = (1.98 * S) - 156.6 \quad r^2 = 0.20 \quad \underline{P} < 0.0001 \quad \textbf{2.3}$$

The slope of equation 2.3 was then used to create the body mass adjustment term bm in equation 2.4.

$$bm = 1.98 * S_d \qquad \textbf{2.4}$$

Size-adjusted body mass BM′ was calculated as:

$$BM' = BM + bm \qquad \textbf{2.5}$$

2.2.3 Captive Redshank

Eight Redshank were held in captivity between August 1992 and May 1993. Four birds were held continuously during this period (individuals W, Y, GW & R), whilst 2 were held from January 1993 onwards (L & N) and a further 2 from March 1993 (RW & G). Equal numbers of *robusta* and *britannica* were always maintained. They were held indoors in aviaries of 2.4m (l) x 1.2m x 1.2 under a simulated ‘normal’ day-length regime and temperature close to ambient. Food was provided *ad libitum* and consisted of commercial pelleted trout food and blow-fly larvae. Fresh water was constantly flowing through the aviaries and was readily available for bathing and drinking.

Each of the captives was weighed to the nearest gram and its body composition measured using TOBEC (see below) at least once every 2 weeks. The number of times an individual was weighed in a single month varied somewhat between individuals and between months. This might have created bias in calculation of the monthly mean of the weights of all the captives. To combat any bias, the group mean was calculated from the monthly averages of the size-adjusted body mass BM′ of each individual captive. This procedure was applied to other measures of body condition (see below).

2.2.4 Measurement of Total Body Electrical Conductivity (TOBEC)

TOBEC was measured using the EM-Scan (3420 Constitution Drive, Spring-field, Illinois 62707, U.S.A.) SA-1 Small Animal Body Composition Analyser. The TOBEC technique involves placing the animal in a measurement chamber which is surrounded by a solenoid. The animal acts as a conductor and alters the electromagnetic inductance of the coil which is measured by changes in the phase relation of voltage and current in a high frequency (5 MHz) signal passed through the coil (Harker, 1973). Thus the change in inductance is proportional to the total electrical conductivity of the animal's body. The electrical conductivity of lipids is only around 4-5% of those of lean tissues, body fluid and bone (Pethig, 1979). Therefore, the primary contributor to the TOBEC will be the total lean mass (TLM).

The SA-1 was used indoors to take TOBEC measurements of captive birds and also used on wild birds in the field when powered by a 12V accumulator via an Oertling PC-01 converter to provide 240V, 50 cycles AC. In both cases, dry birds (see Scott *et al.*, 1991) of assumed normal hydration (see Walsberg, 1988) and not wearing metal leg-rings (Scott *et al.*, 1991) were restrained using a soft plastic cylindrical jacket with Velcro fastenings before inserting each in turn, into the measurement chamber. TOBEC readings were taken with the chamber empty (E) and then with the bird in the chamber (S) and repeated 4 times. A reference number (R) was taken before and after each set of readings. The TOBEC index (I) was calculated according to equation 2.6.

$$I = a^*[(S - E)/R] \qquad \textbf{2.6}$$

where a is a normalisation constant provided by EM-Scan and peculiar to each machine ($a = 0.9883$ in this case). The TOBEC readings are greatly affected by the horizontal position of the bird within the measurement chamber, whereas vertical position is not important (Scott *et al.*, 1991). The strongest and most uniform part of the magnetic field generated by the solenoid of the SA-1 is halfway along the measurement chamber, hence some studies (Morton *et al.*, 1991; Skagen *et al.*, 1993; Meijer *et al.*, 1994) maintained each bird at the same position relative to the centre of the chamber. However, Scott *et al.* (1991) found that the optimum position along the measurement chamber varied slightly with the size and shape of the bird, which might change during periods of e.g. fat deposition. In my study Redshank were inserted into the chamber on a Perspex rule head first and keel down, until a maximum value for (S - E) was obtained.

Predicted total lean mass PTLM was calculated from equation 2.7 which was derived using carcass analysis (see Appendix II).

$$PTLM = (0.288 * I) + 55.5 \qquad \textbf{2.7}$$

Predicted mass of fat PFM was calculated by subtracting PTLM from BM (equation 2.8).

$$PFM = BM - PTLM \qquad \textbf{2.8}$$

Both PTLM and PFM were calculated with a mean error of ±4.3g (95% CI=2.4g) which proved to be of sufficient resolution for the purposes of my study (see Appendix II).

2.2.5 Seasonal changes in body composition

Between October 1992 and April 1995 the body composition of 275 adult Redshank was measured in the field using TOBEC. During catching, the birds were often slightly splashed with seawater and thus could not be introduced into the SA-1 immediately after capture since wet plumage increases TOBEC (Scott *et al.,* 1991). It was also suspected that residual salt on the feathers of dry birds would cause an increase in TOBEC. However, experiments on captive birds which were immersed in artificial seawater (33 ppt Na Cl solution) (and were wetter than would be expected after catching) showed that one hour's drying in a large hessian sack was sufficient to remove any effect of the salting on TOBEC. Hence in the field, all birds which had even slightly wet plumage at capture were allowed to dry in hessian sacks or in hessian-lined keeping cages for at least 1 hour before measuring TOBEC. In contrast, TOBEC was measured immediately after capture in birds which were either caught dry in cannon nets or caught in mist nets. TOBEC measurements were not taken from birds held more than 3 hours after capture because they might have become slightly dehydrated (Davidson, 1984).

To control for body size differences between individuals and between races, PFM was divided by TBM and expressed as a percentage to give a Lipid Index (LI). PTLM was size-adjusted in a manner similar to BM (section 2.2.2). PTLM was regressed (Equation 2.9) against the size-factor S derived from eqn. 2.1 for 275 wild adult Redshank, and the slope was combined with S_d (see eqn. 2.2) to create an adjustment ptlm (Equation 2.10) to each PTLM.

$$PTLM = (1.495 * S) - 101.9 \quad r^2 = 0.27 \quad \underline{P} < 0.05 \quad \mathbf{2.9}$$

$$ptlm = 1.495 * S_d \quad \mathbf{2.10}$$

Size-adjusted PTLM, PTLM' is therefore:

$$PTLM' = PTLM+ptlm \quad \mathbf{2.11}$$

2.2.6 Comparison of body composition of wild and captive Redshank

The stomachs, intestines, livers and complete pectoral muscle blocks (pectoralis major and supracoracoideus) were dissected from 7 captive Redshank and from 4 Redshank which had been killed accidentally during cannon-netting. Two of the wild birds were killed on 11/8/93 and the others on 2/11/93 and all were sealed in plastic bags and frozen. Two of the captives were killed on 12/12/94, one on 13/12/94, one on 25/12/95 and four on 5/5/95, after all had been kept for 2-3 months. All organs were weighed immediately after dissection to the nearest mg on a torsion balance. Following dissection of the left pectoral muscle block, four skeletal measurements were taken to the nearest 0.1mm using vernier callipers according to the methods of Piersma *et al.* (1984) in order to calculate a standard muscle volume SMV (Evans & Smith, 1975). The mass of one pectoral muscle block was then expressed as a proportion of the SMV to produce an index of muscle size independant of total body (skeletal) size.

Table 2.1: Definitions and abbreviations of terms of body composition

Abreviation	Definition
BM	Total body mass
BM′	Size-adjusted total body mass
TOBEC	Total body electrical conductivity; or index of TOBEC produced by EM-Scan SA1 Small Body Composition Analyser
TLM	Total lean (fat-free) mass
PTLM	Total lean mass predicted by the regression of TLM against TOBEC
PTLM′	Size-adjusted PTLM
FM	Lipid mass = BM - TLM
PFM	Predicted lipid mass = BM - PTLM
LI	Lipid Index = 100 * FM/BM
PLI	Predicted lipid index = 100 * PFM/BM

2.3 Results

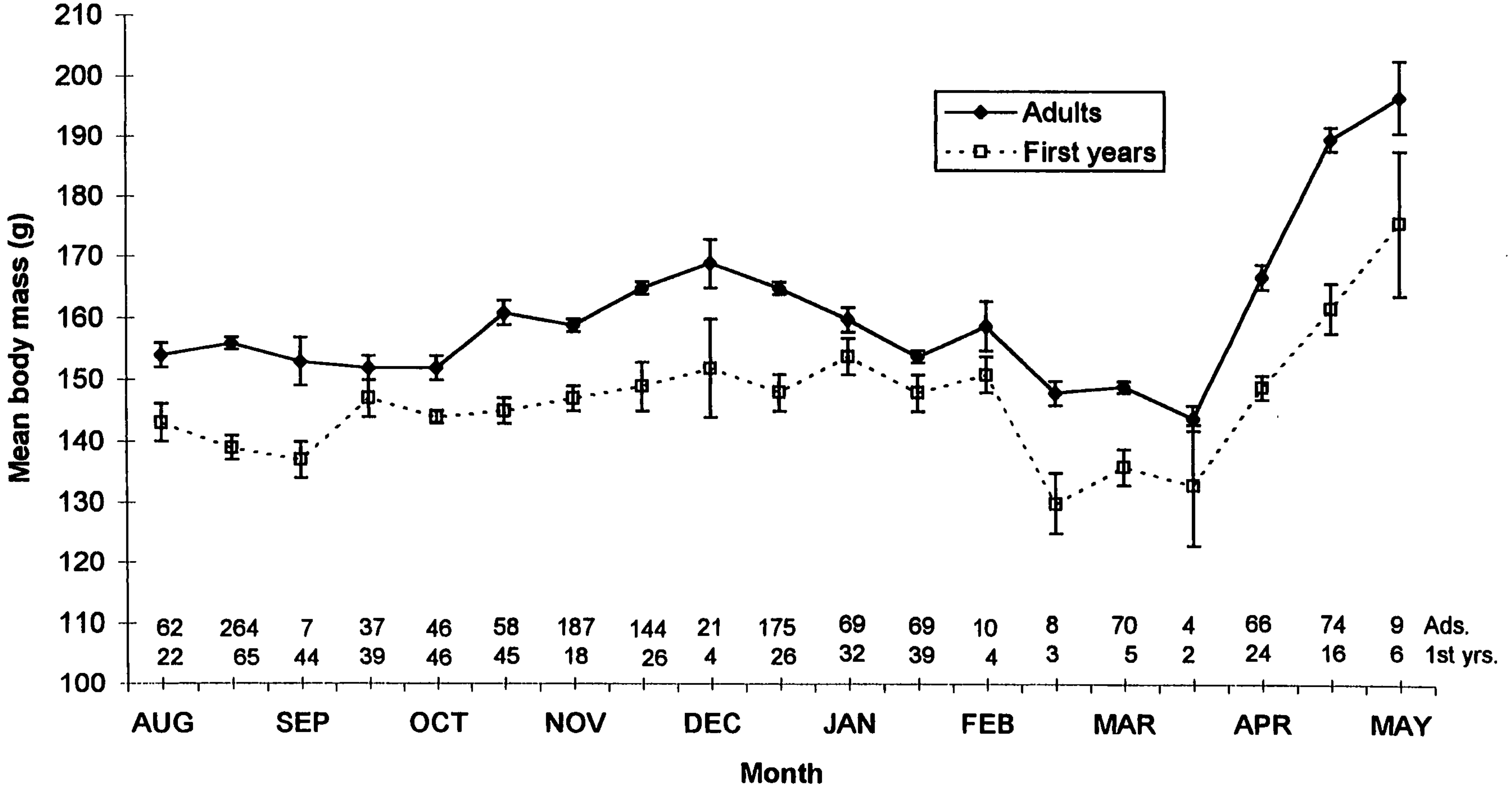
2.3.1 Seasonal changes in mean body mass of adult and first year Redshank at Teesmouth

There was sufficient data on BM of wild adult and first year Redshank at Teesmouth from 1983-1995 to produce mean BM values for first and second halves (early and late) of each month (Figure 2.1). Adult Redshank were significantly heavier than first years (ANOVA $F_{1,1863} = 104$, $P < 0.0001$), but BM of both age groups varied significantly with month (ANOVA $F_{21,1383} = 38.7$, $P < 0.0001$ for adults; $F_{21,437} = 6.17$, $P<0.0001$ for first years).

Adult Redshank maintained constant BM during August and September before increasing from late October onwards. BM from late November through December was significantly greater than in the preceding months and in the subsequent period up until late March (Student-Newman-Keuls (SNK) Multiple Range Test $P < 0.05$). Peak mean BM in December represented an increase of 8.6% on the September mean. BM decreased through January, February and early March by 9.7% of the December mean, a significant drop (SNK Test $P < 0.05$). BM rose steeply and significantly (SNK $P < 0.05$) in April to 32% above the March mean by early May.

Unlike adult Redshank, first years did not exhibit a significant mid-winter peak in BM, which remained constant between late September and early February (SNK >0.05). The decline in BM during late February and March was also not significant (SNK>0.05). BM of first years showed a significant increase (SNK<0.05) through April and by early May was 24% higher than in late March.

Figure 2.1: Mean fortnightly body masses of adult and first year Redshank at Teesmouth (1983/84-94/95). Numbers indicate sample size and error bars denote 2xSE.



2.3.2 Seasonal changes in mean body mass of races of adult Redshank at Teesmouth

Around 77% of Redshank caught and measured in a given month could be assigned to a race at above the 70% level of probability (Figure 2.2a). Figure 2.2b shows the relative proportions of *robusta* and *britannica* as percentages of those birds which could be assigned to a race in each month. In August *britannica* predominated 7:3, but the proportion gradually decreased through September and October; *robusta* predominated at around 6:4 between November and April. The association between month and the proportions of *robusta* and *britannica* was significant ($\chi^2_{16} = 73.1$, $P<0.001$; see Table 2.2)

These seasonal changes in the proportions of both races had important implications for interpretation of the overall pattern of monthly mean BM in Adult Redshank at Teesmouth. The mid-winter peak in Adult size-adjusted body mass BM′ in December was only 5.2% above the September mean (Figure 2.3), (whereas it had been 8.6% in BM). Overall, however, there was no significant difference between fortnightly mean BM and BM′ (Paired t-test $t_{12} = 1.067$, $P > 0.05$). Like BM, BM′ also showed significant variation with month (ANOVA $F_{16, 616} = 43.4$ $P<0.0001$) and a pattern of change similar to BM (Figure 2.3).

Figure 2.4 shows significant seasonal changes in mean monthly BM of *robusta* and *britannica* (ANOVA $F_{8, 165} = 14.5$ $P < 0.0001$ for *britannica*; $F_{8, 304} = 37.6$ $P < 0.0001$ for *robusta*). In all periods *robusta* were significantly heavier than *britannica* (ANOVA $F_{1, 486} = 13.5$, $P < 0.0001$), but their monthly mean BMs were significantly correlated (Spearman Rank Correlation $r_{S, 8} = 0.813$, $P < 0.005$). The BM of *robusta* in November was 7.8% above the September mean, which was in turn, significantly greater (SNK $P < 0.05$) than those in August, January and

Figure 2.2a: Proportions of *robusta, britannica* and Redshank of unknown race of those caught and measured at Teesmouth (1983/84-94/95).

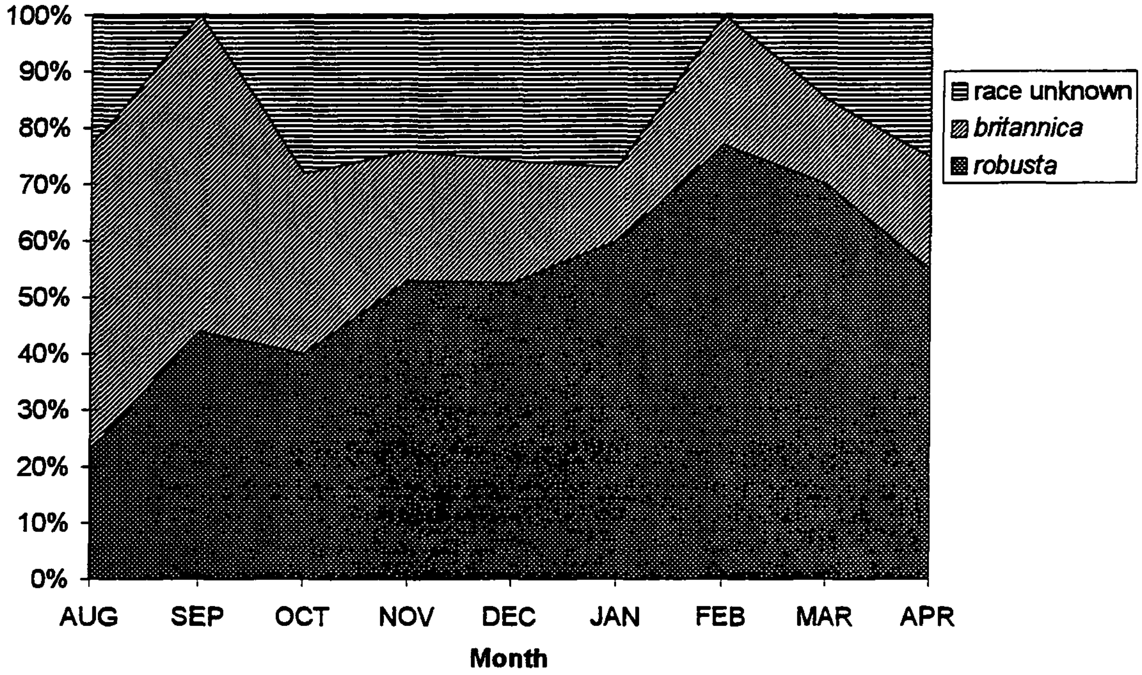


Figure 2.2b: Proportions of *robusta* and *britannica* of those Redshank caught at Teesmouth (1983/84-94/95) that could be assigned to a race.

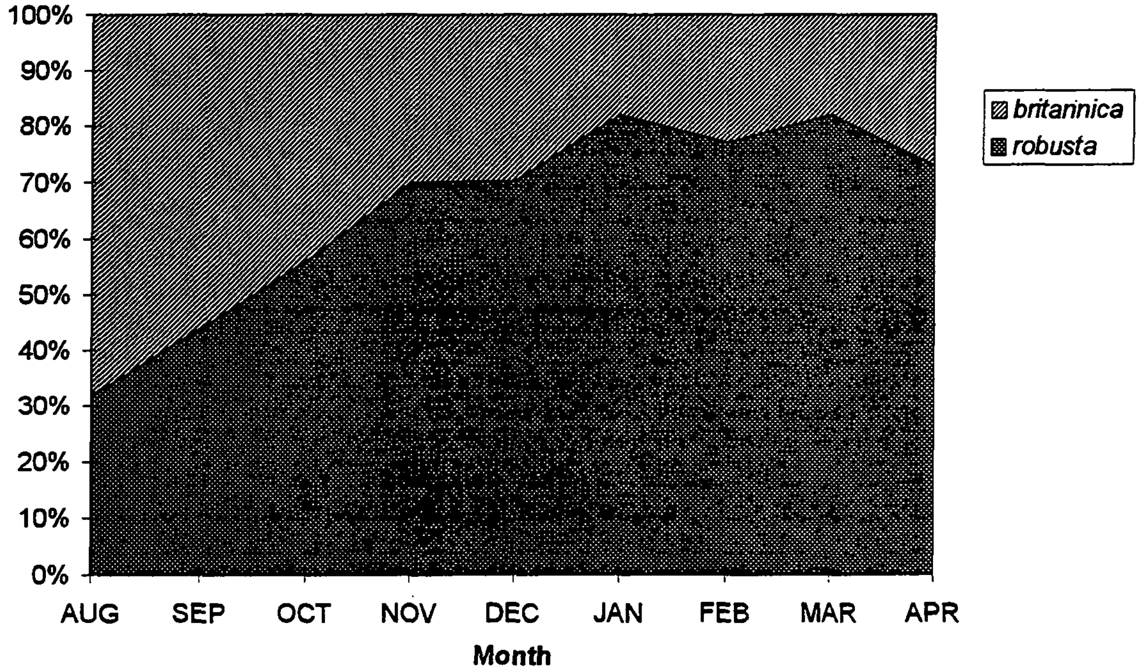


Table 2.2: Chi-squared contingency table of numbers of Redshank caught at Teesmouth between 1983-1995 which were identified as either *robusta* or *britannica*, or could not be assigned to a race with >70% confidence using the discriminant function formulae of Summers *et al.* (1988); where O = observed, E= expected, and figures in bold = $(O - E)^2/E$. There was a significant association between the proportion of *robusta* and *britannica* in the population and month ($\chi^2_{16} = 73.1$, $P<0.001$).

	AUG	**SEP**	**OCT**	**NOV**	**DEC**	**JAN**	**FEB**	**MAR**	**APR**	**Total**
robusta	O=26 E=56.4 **16.4**	0=4 E=4.5 **0.06**	O=10 E=12.4 **0.46**	O=103 E=95.4 **0.62**	O=51 E=48 **0.19**	O=18 E=14.8 **0.69**	O=10 E=6.4 **2.03**	O=33 E=23.2 **4.14**	O=58 E=51.9 **0.72**	**313**
britannica	O=62 E=31.3 **30.1**	O=5 E=2.5 **2.5**	O=8 E=6.9 **0.18**	O=43 E=53.1 **1.92**	O=21 E=26.7 **1.22**	O=4 E=8.2 **2.15**	O=3 E=3.6 **0.1**	O=7 E=12.9 **2.7**	O=21 E=28.9 **2.16**	**174**
race unknown	0=26 E=26.3 **0.003**	O=0 E=2.1 **2.1**	O=7 E=5.8 **0.25**	O=47 E=44.5 **0.14**	O=25 E=22.4 **0.3**	O=8 E=6.9 **0.18**	O=0 E=3 **3**	O=7 E=10.8 **1.34**	O=26 E=24.2 **0.13**	**146**
Total	**114**	**9**	**25**	**193**	**97**	**30**	**13**	**47**	**105**	**633**

Figure 2.3: Mean fortnightly body mass (BM) and size-adjusted body mass (BM') of Redshank at Teesmouth (1983/84-94/95). Error bars denote 2xSE and numbers indicate sample size.

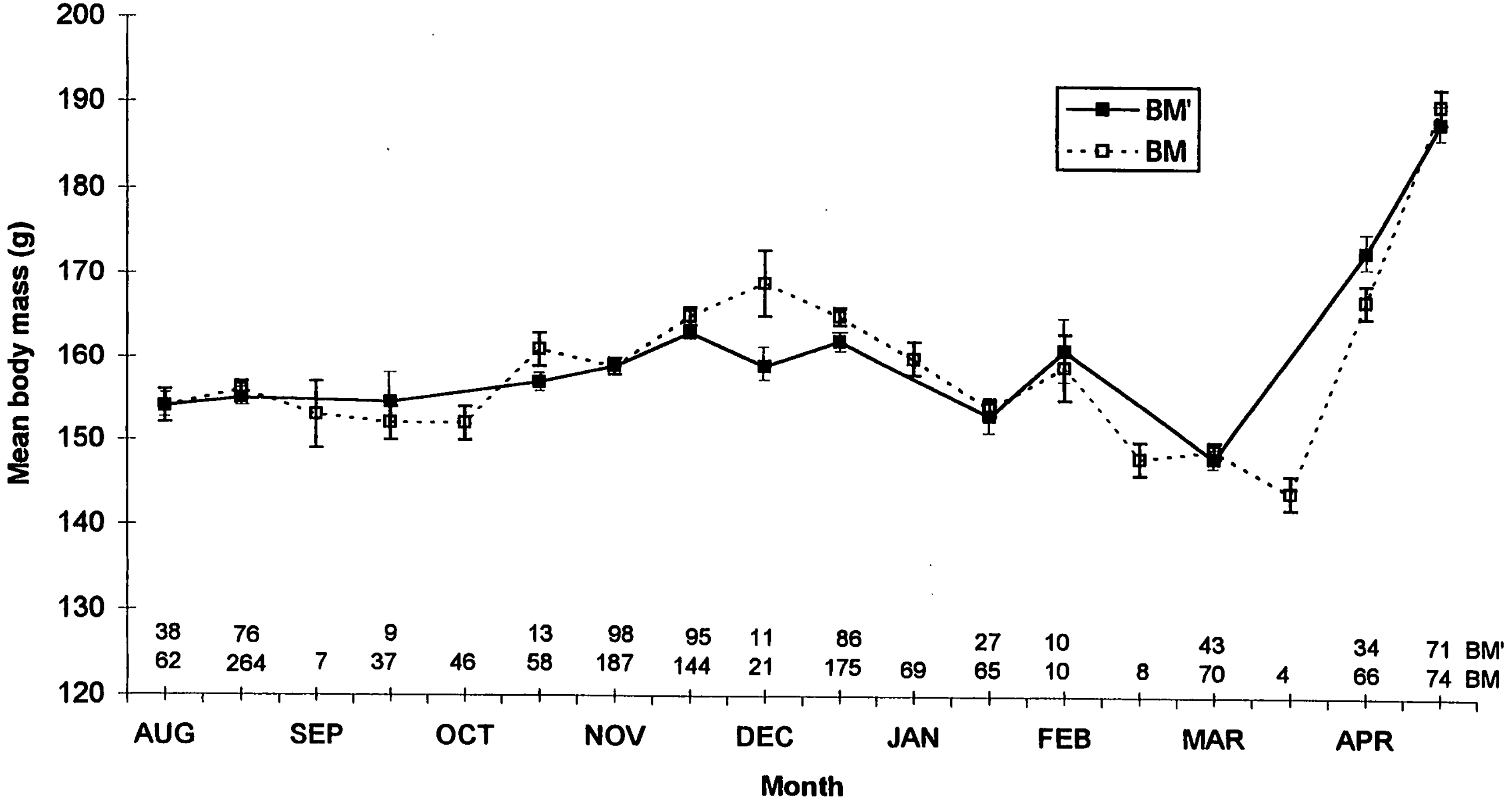
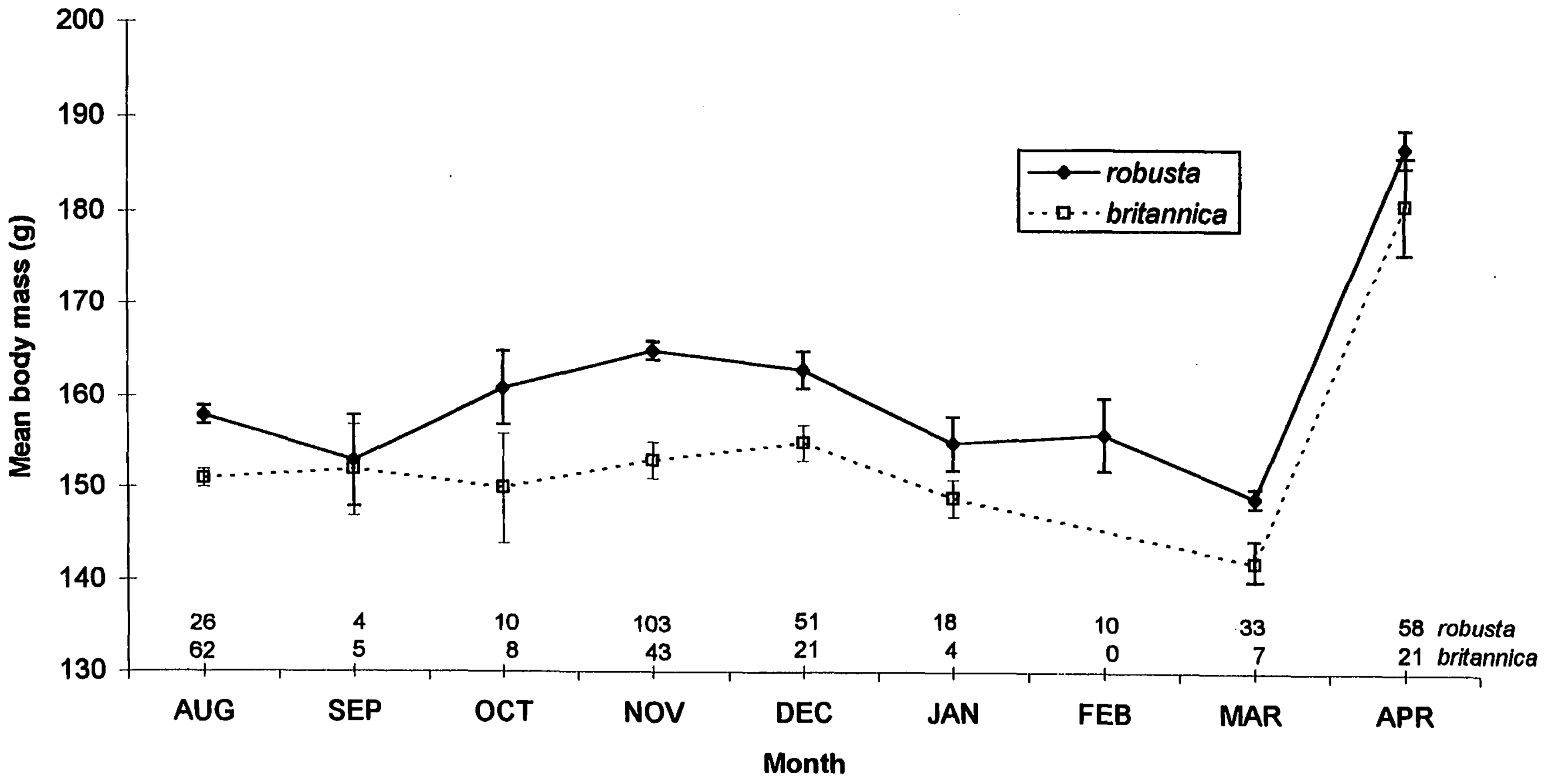


Figure 2.4: Mean monthly body masses of races of Redshank at Teesmouth (1983/84-94/95). Numbers indicate sample size and error bars denote 2xSE.

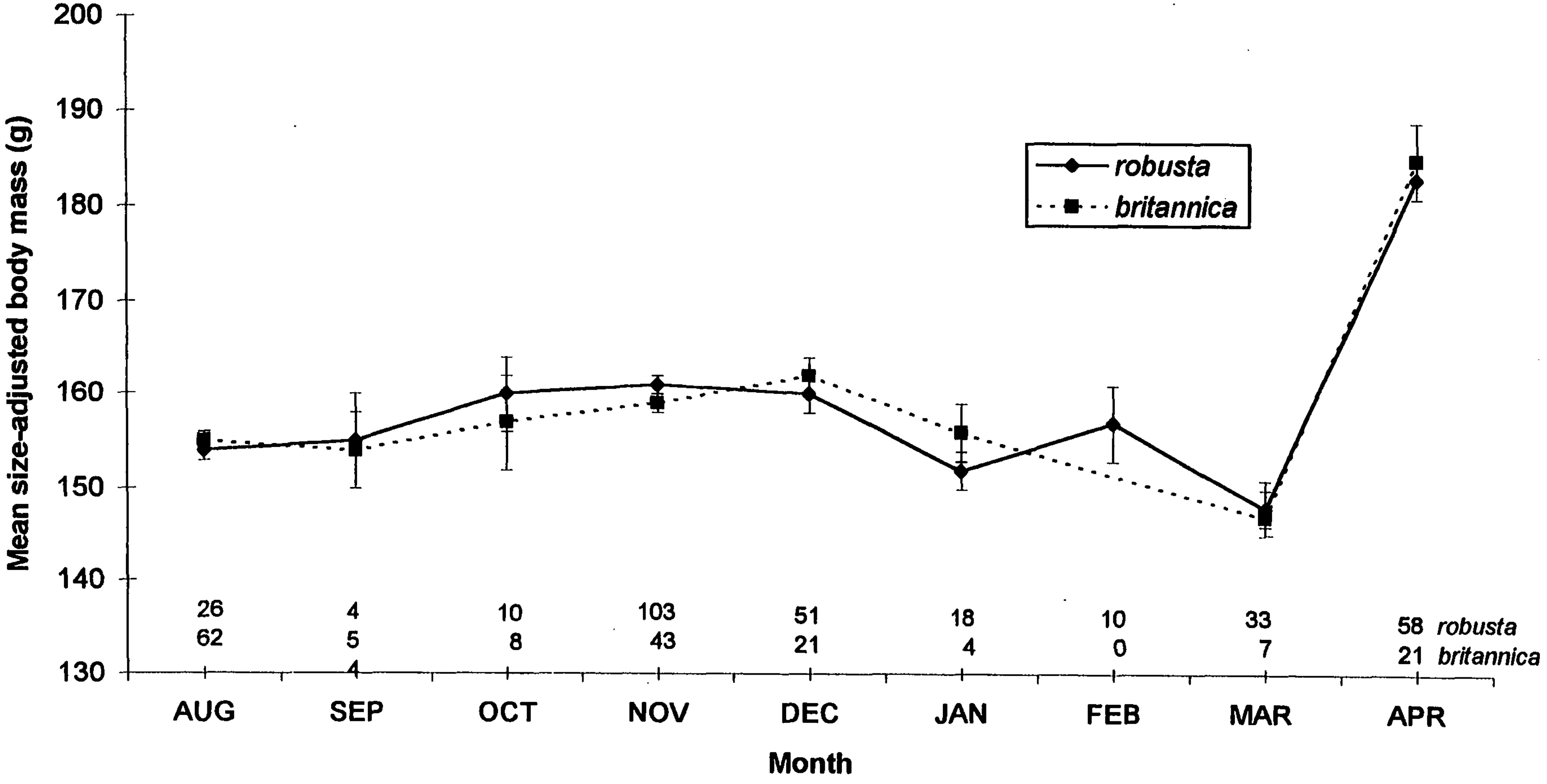


March when BM fell by 9.7% of the November mean. However, *britannica* did not show any significant mid-winter peak in BM and although BM fell in March by 8.1% compared to December, this fall was not significant (SNK $P > 0.05$). In April both *robusta* and *britannica* showed significant (SNK $P < 0.05$) and substantial increases in BM, of 25.5% and 27.5% respectively above the March means.

When the monthly mean BMs of the two races were adjusted for body size (Figure 2.5), they were not significantly different (ANOVA $F_{1,486} = 0.658$ $P > 0.05$), indicating that the relative seasonal gains and losses in BM of *robusta* and *britannica* were similar. Variation in body size in the monthly samples of *britannica* had a considerable effect on mean monthly BM, in that when the effect of size was removed, BM′ not only showed significant variation with month (ANOVA $F_{8,165} = 19.45$, $P < 0.0001$) but exhibited a significant peak in BM′ in December of 5.2% over the September mean (SNK $P < 0.05$). Also, the fall in BM′ in March of 9.3% (of the December mean) was significant (SNK $P < 0.05$).

Variation in monthly mean BM′ of *robusta* (Figure 2.5) was also significant (ANOVA $F_{8,304} = 37.6$ $P < 0.0001$) and showed the same pattern of change as BM, though the peak in BM′ in November was only 3.9% greater than the September mean. In April both *robusta* and *britannica* showed significant (SNK $P < 0.05$) and substantial increases in BM′ of 23.6% and 25.9% respectively above the March means.

Figure 2.5: Mean monthly size-adjusted body masses of races of Redshank at Teesmouth (1983/84-94/95). Numbers indicate sample size and error bars denote 2xSE.



2.3.3 Seasonal changes in body mass of individual Redshank at Teesmouth

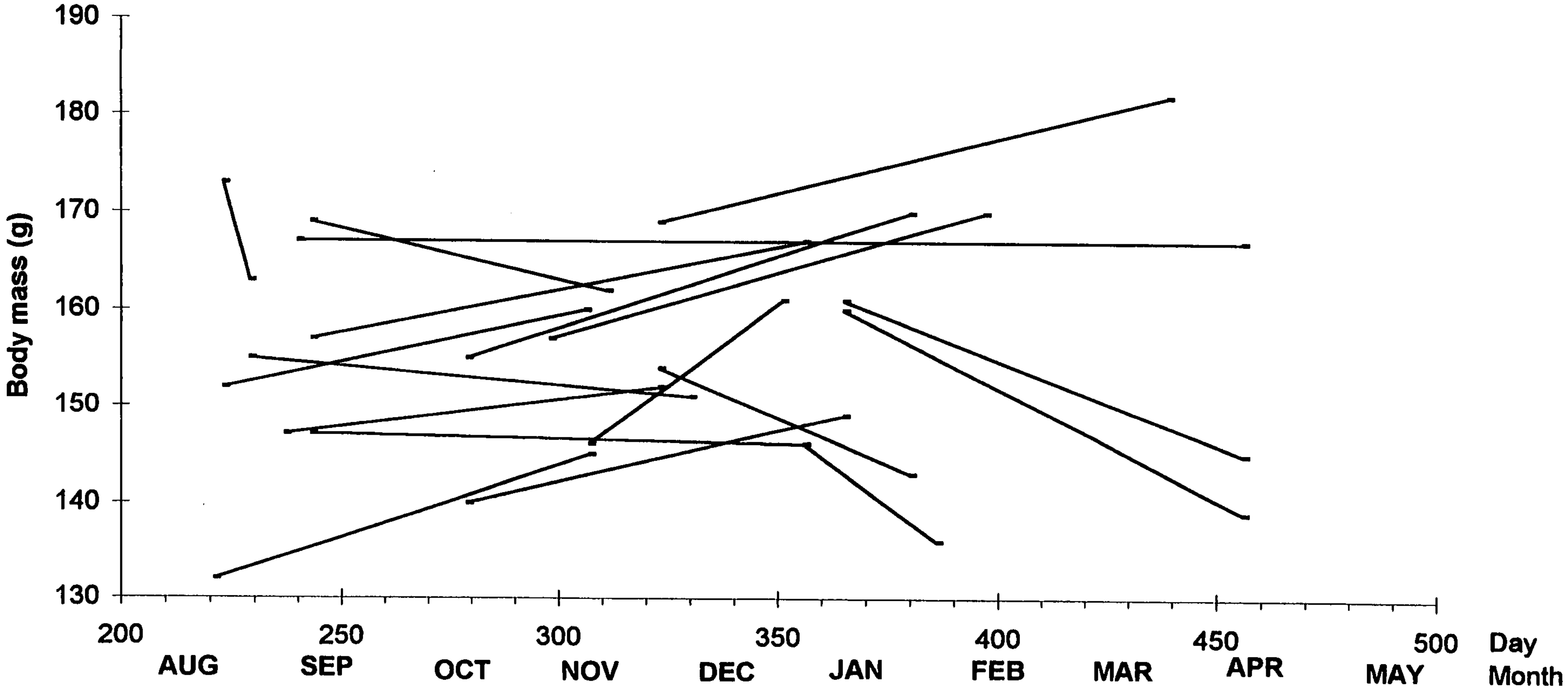
Figures 2.6 and 2.7 show changes in BM of individual Redshank (n=17 for unknown race (Figure 2.6), n=15 for *robusta,* n=5 for *britannica* (both Figure 2.7)) caught and recaught once or twice between August and including 1 April during the same non-breeding season at Teesmouth. In general, changes in BM of individuals paralleled changes in mean body mass of the population (Figures 2.1, 2.3-2.5) irrespective of race (Figure 2.7). Figure 2.8 shows that individual Redshank recaptured after 1 April (n=2 for unknown race, n=9 for *robusta*, n=3 for *britannica*), regardless of race, had substantially higher BMs compared to earlier in the same season.

The rate of change of BM in individuals and the mean adult BM′ for the Teesmouth population were compared using the following procedure: the difference d_2 between an individual's BM at recapture and the monthly mean BM′ at the same time was compared with the difference d_1 between individual BM and mean BM′ at first capture using the Wilcoxon paired sample test. A significant difference between d_1 and d_2 would indicate a different rate of change in BM between an individual's and the population mean. However, the changes in mean BM′ of the population were representative of individual changes of *robusta, britannica* and birds of unknown race (Wilcoxon paired-sample test $T_8 = 15.5$, $P > 0.05$ for *britannica*; $T_{24} = 120$, $P>0.05$ for *robusta*; $T_{19} = 72.5$, $P>0.05$ for birds of unknown race).

2.3.4 Comparison of seasonal changes in body mass of captive and wild Redshank

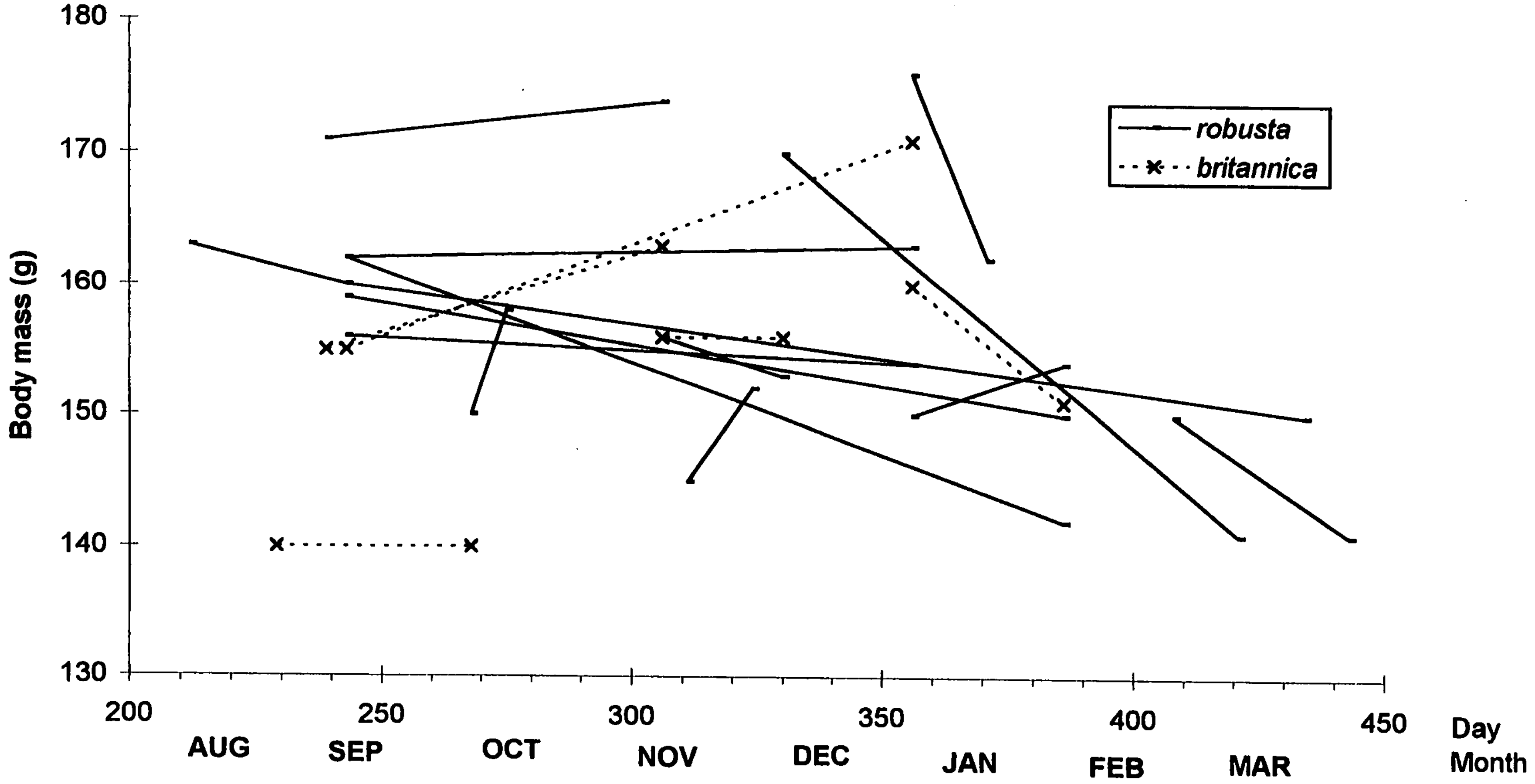
The fortnightly means of the average BM′ of each of the eight captive Redshank

Figure 2.6: Changes in body mass of individual Redshank of unknown racial origin caught and recaptured at Teesmouth between August and March during the same non-breeding season (1988/89-1994/95).



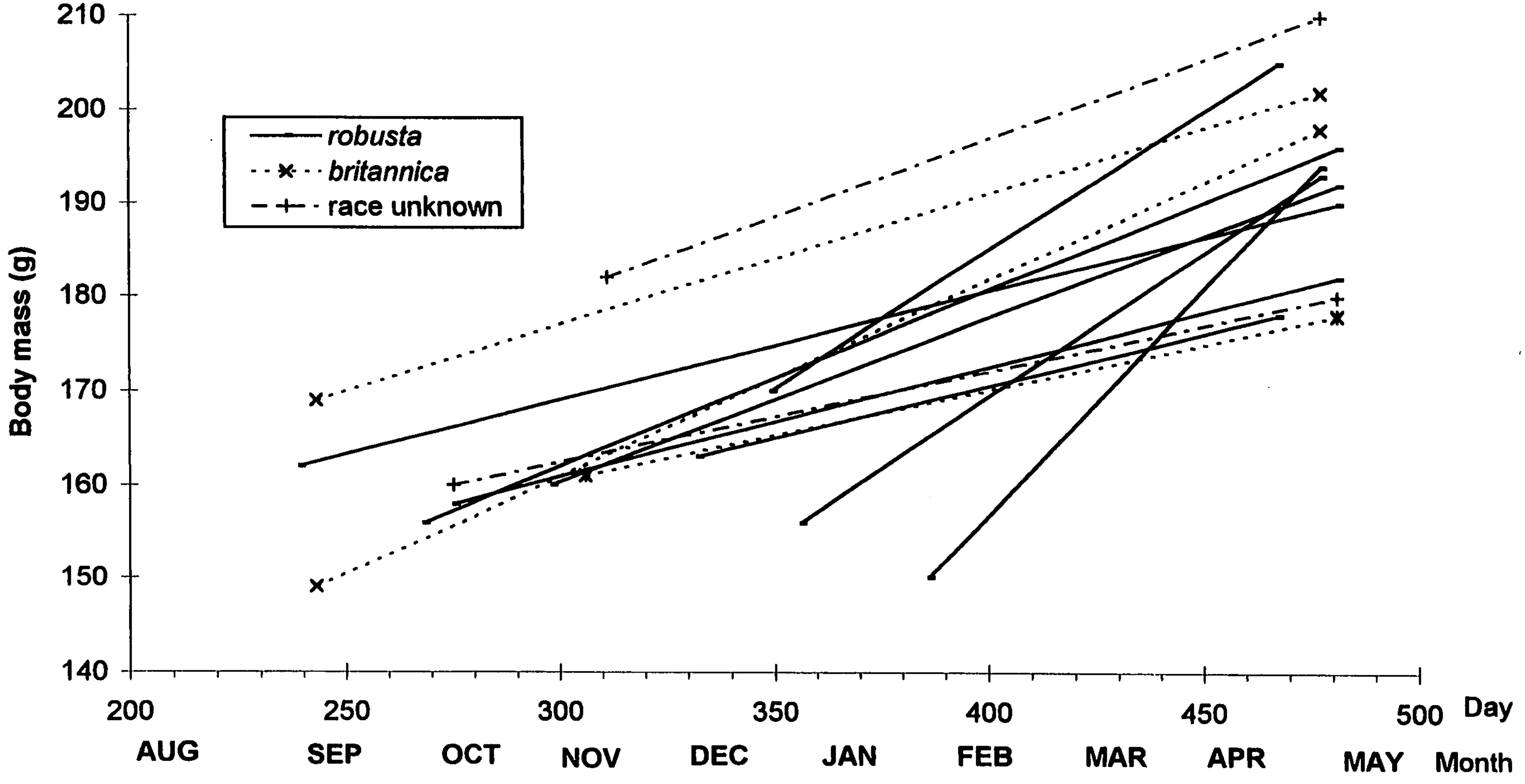
Day=1 (e.g. 1988/89 season) on 1 Jan 1988 and Day=455 on 31 Mar 1989.

Figure 2.7: Changes in body mass of individual Redshank caught and recaptured at Teesmouth between July and March during the same non-breeding season (1992/93-1994/95).



Day=1 (e.g. 1992/93 season) on 1 Jan 1992 and Day=455 on 31 Mar 1993.

Figure 2.8: Changes in body mass of individual Redshank recaptured at Teesmouth during April and May following capture earlier in the same non-breeding season (1992/93-1994/95).



Day=1 (e.g. 1992/93 season) on 1 Jan 1992 and Day=455 on 31 Mar 1993.

from early August to late April were significantly correlated with fortnightly means BM′ of wild Redshank at Teesmouth (Figure 2.9) (Spearman Rank Correlation $r_{s,13} = 0.816$, $P < 0.001$). There was also a significant correlation between the mean BM′ of wild Redshank and of the four captives which were held continuously throughout this period (Spearman Rank Correlation $r_{s,13} = 0.620$, $P < 0.02$). During the period from early November to late April there was no significant difference between the mean BM′ of the captives and wild Redshank (Paired t-test $t_8 = 2.063$, $P > 0.05$ for 8 captives; $t_8 = 1.524$, $P > 0.05$ for 4 captives). However, the means of BM′ for the 4 captives held during the period from early August to late October were significantly less than those of the wild birds (Paired t-test $t_3 = 6.159$, $P<0.01$).

Figure 2.10 shows changes in fortnightly mean BM for each individual captive; individuals in figures 2.10a,b,e,h are *robusta* whilst the remainder are *britannica*. All but one of the four birds which were kept from August through to May (Figure 2.10a-d) showed seasonal variations in BM which were significantly correlated with mean fortnightly BM′ of wild Redshank at Teesmouth (Spearman Rank Correlation $r_{s,13} = 0.530$, $P < 0.05$ for W; $r_{s,12} = 0.702$, $P < 0.01$ for Y; $r_{s,13} = 0.418$, $P>0.05$ for GW; $r_{s,13} = 0.528$, $P < 0.05$ for R). The relative increase in BM during the first part of winter was greater in the captives than in wild Redshank (Table 2.3), since BM of the captives was maintained at such a low level during August and September. However, the decrease in BM in the captives in March relative to the mid-winter peak was comparable with that in wild Redshank at Teesmouth. All the captives, regardless of race, showed substantial increases in BM during April and May (Figure 2.10), though individuals W and L (both robusta) started to increase in BM during March (Figure 2.10a & e). The relative increases during this period were consistently lower in those captives which were kept from August to May (W, Y, GW, R) (Table 2.3).

Figure 2.9: Mean fortnightly size-adjusted body mass of wild Redshank at Teesmouth (1983/84-94/95) and captive Redshank. Spearman Rank Correlation r_s=0.816 P<0.001. Error bars indicate 2xSE.

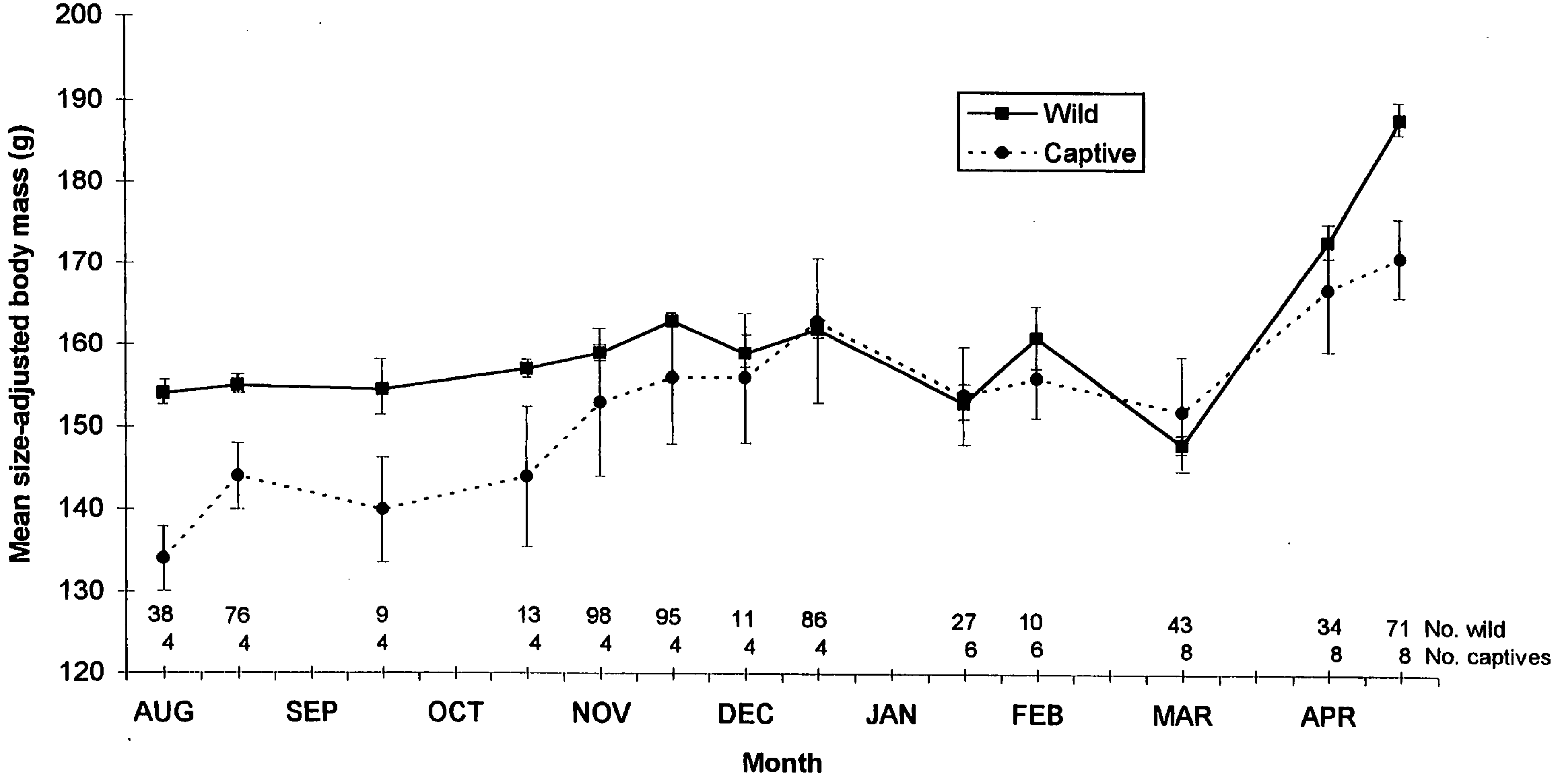
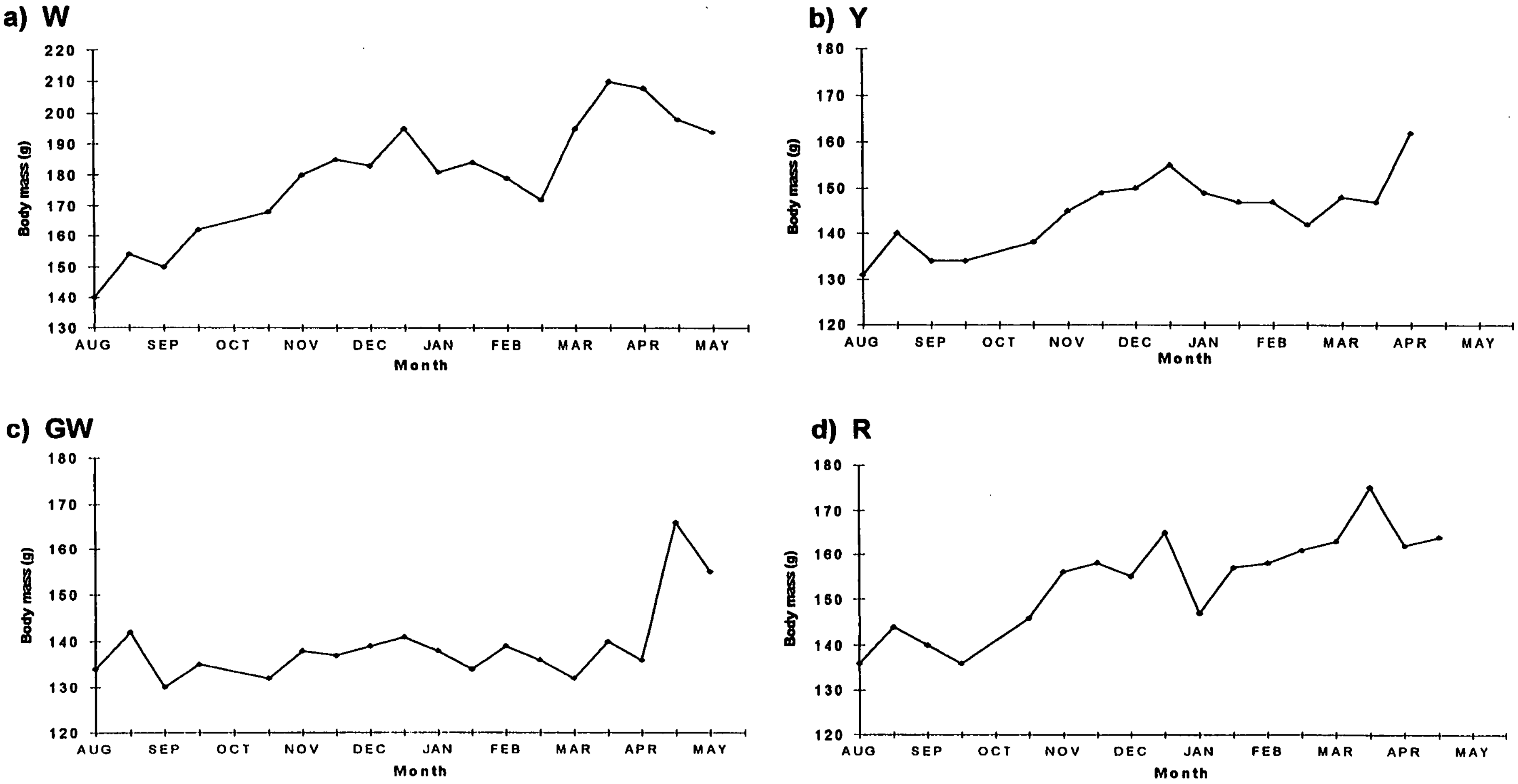
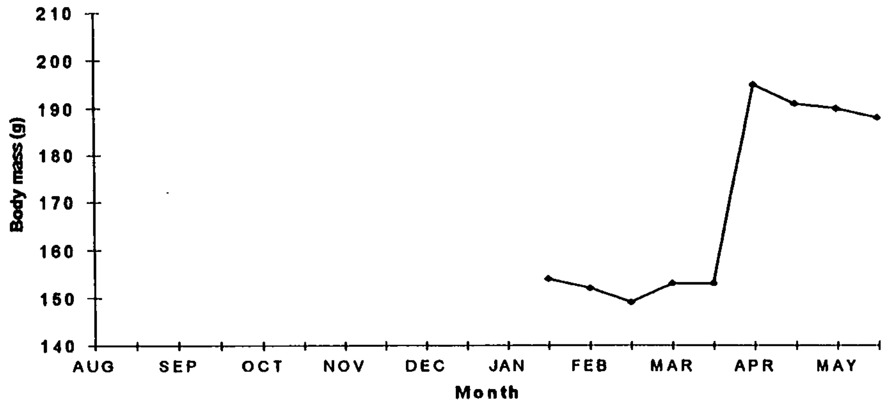


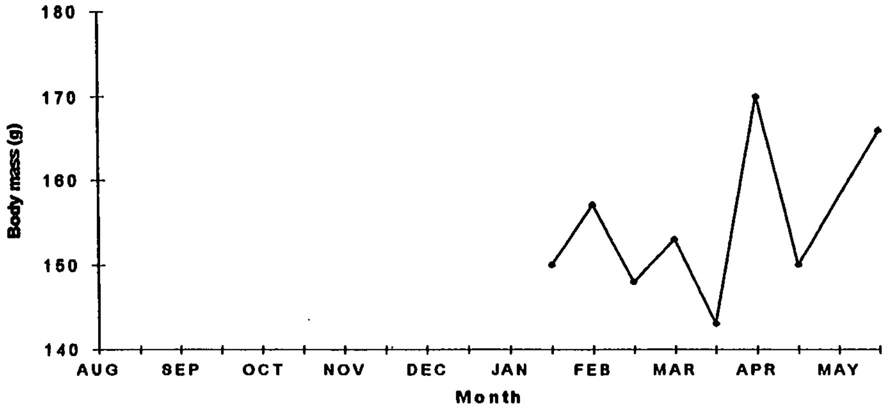
Figure 2.10: Fortnightly mean body mass in individual captive Redshank.



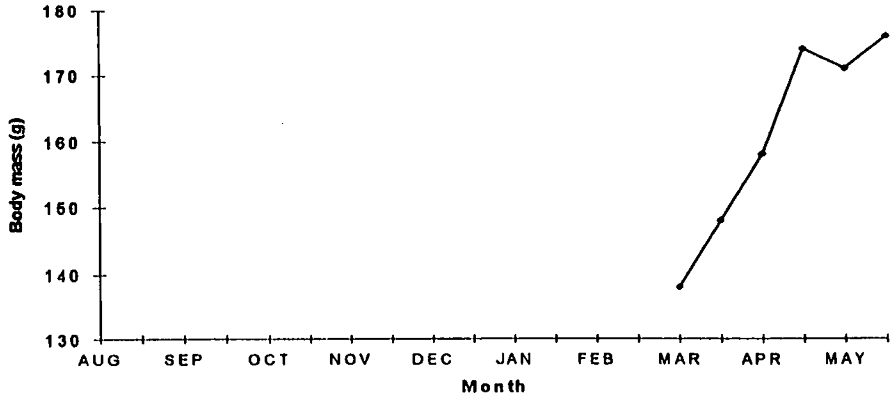
e) L


Body mass (g)
210
200
190
180
170
160
150
140
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
Month

f) N


Body mass (g)
180
170
160
150
140
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
Month

g) G


Body mass (g)
180
170
160
150
140
130
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
Month

h) RW

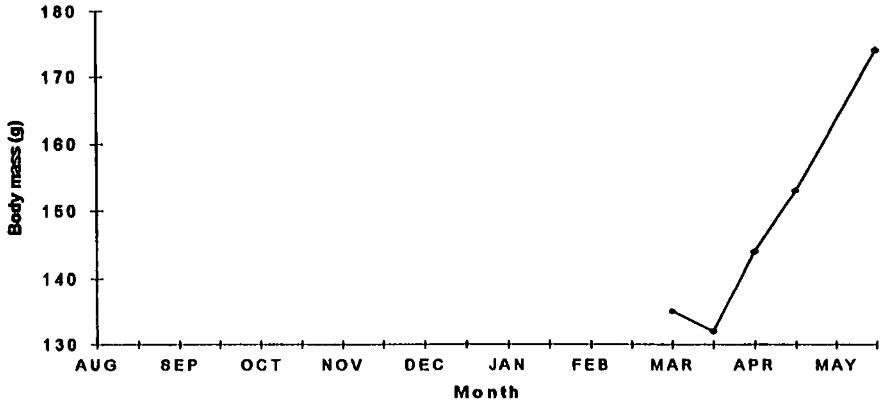

Body mass (g)
180
170
160
150
140
130
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
Month

Table 2.3: Relative seasonal changes in body mass (BM) and size-adjusted body mass (BM′) of groups of wild Redshank at Teesmouth and 8 captive individuals (W, Y, L and G are *robusta;* GW, R, N and RW are *britannica*).

	†Mid-winter increase %	‡Late-winter decrease %	*Spring Increase %
Wild mixed-race BM	8.6	9.7	32.0
Wild mixed-race BM′	5.2	8.6	27.0
***robusta* BM**	7.8	9.7	25.5
***robusta* BM′**	3.9	8.1	23.6
***britannica* BM**	2.0	8.4	27.5
***britannica* BM′**	5.2	9.3	25.9
Captive individuals BM:			
W	30.0	8.2	16.2
Y	15.6	8.4	14.1
GW	8.5	6.4	25.7
R	21.3	1.2	7.4
L	-	-	27.5
N	-	-	25.8
RW	-	-	32.0
G	-	-	27.5

† Difference between September mean and peak mean in November or December as a percentage of the former.

‡ Difference between peak mean in November or December and March mean as a percentage of the former.

* Difference between March mean and peak mean in April or May as a percentage of the former.

2.3.5 Seasonal changes in body composition of Redshank at Teesmouth

On 25 September and 25 October 1993 when birds were caught both dry and wet, there was no significant difference in TOBEC index I (T-test $P>0.05$) between the dry birds ($n=5$ on 25 September, $n=4$ on 25 October) and those caught on the same day which were wet and then dried ($n=18$ on 25 September, $n=24$ on 25 October). On both days, body mass of the 'wet' and 'dry' birds was not significantly different (T-test $P>0.05$).

Monthly mean PTLM of adult Redshank of mixed race (Figure 2.11) varied significantly with month (ANOVA $F_{8,243} = 7.327$ $P < 0.0001$) in that mean PTLM was significantly greater in both August and April (147g and 143g respectively) than in the other months (SNK $P < 0.05$) in which mean PTLM varied non-significantly between 132g and 137g. This was not attributable to the presence of larger birds during August and April, since PTLM′ showed the same significant seasonal variation (Figure 2.11) (ANOVA $F_{7,215} = 9.346$ $P < 0.0001$; SNK $P < 0.05$).

Monthly mean PFM showed a significant mid-winter peak of 29g in November. Monthly mean PFMs from October through to February were significantly higher than in August when the mean was only 8g (ANOVA $F_{8,243} = 26.843$ $P < 0.0001$; SNK $P < 0.05$). The highest monthly mean of 41g was recorded in April. The seasonal variation in PFM was not attributable to the presence of larger birds in mid-winter or April since mean predicted lipid index (PLI see Table 2.1), as opposed to mass of fat, showed the same significant monthly variation (arcsine-transformed ANOVA $F_{8,241} = 27.941$ $P < 0.0001$; SNK $P < 0.05$) (Figure 2.12). PLI rose from 6% in August to 18% in November, then fell to 9% in March before rising to a peak of 25% in late April.

Figure 2.11: Predicted total lean mass (PTLM) and size-adjusted total lean mass (PTLM') of adult Redshank at Teesmouth 1992/93-94/95. Error bars indicate 2xSE. Numbers denote sample size.

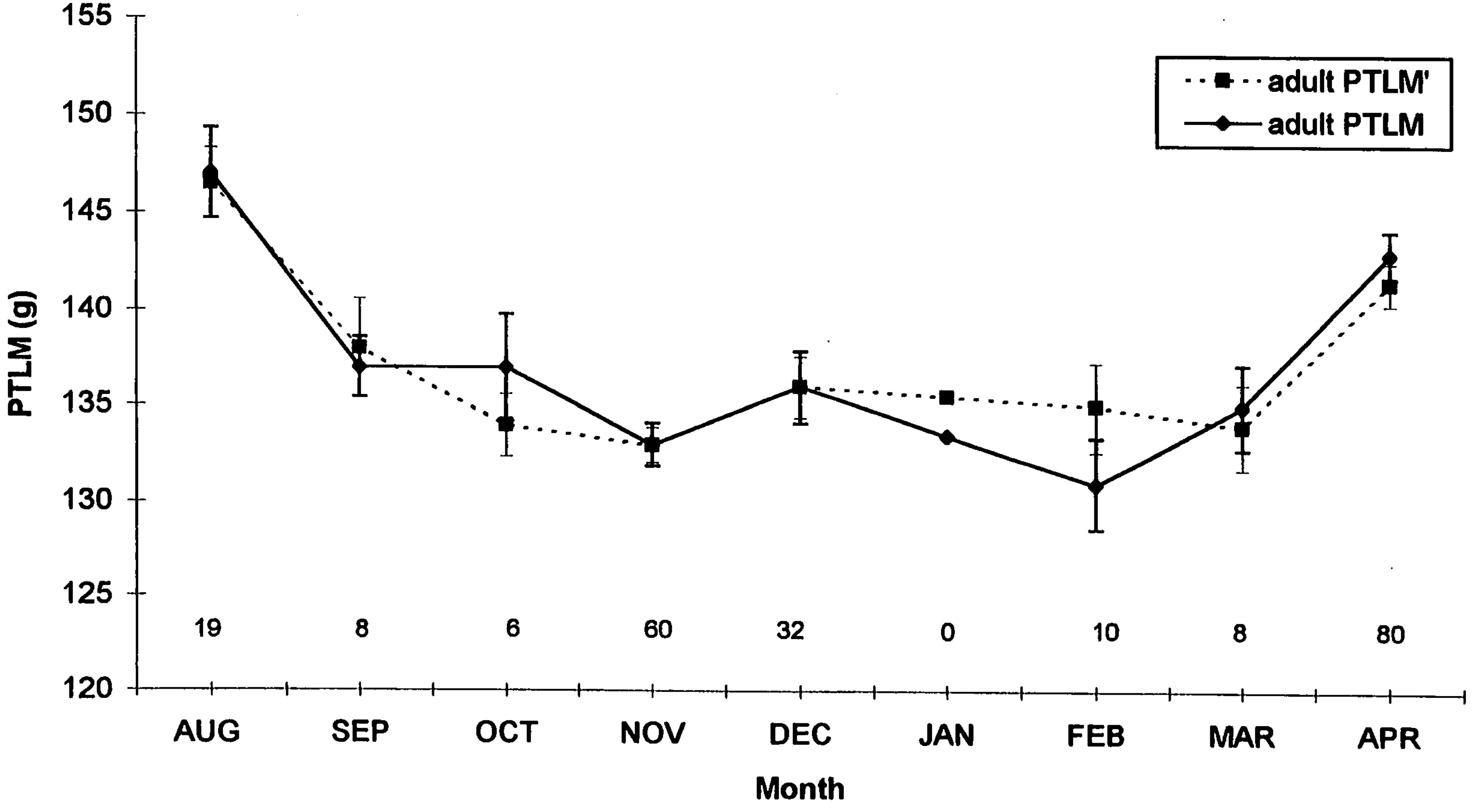
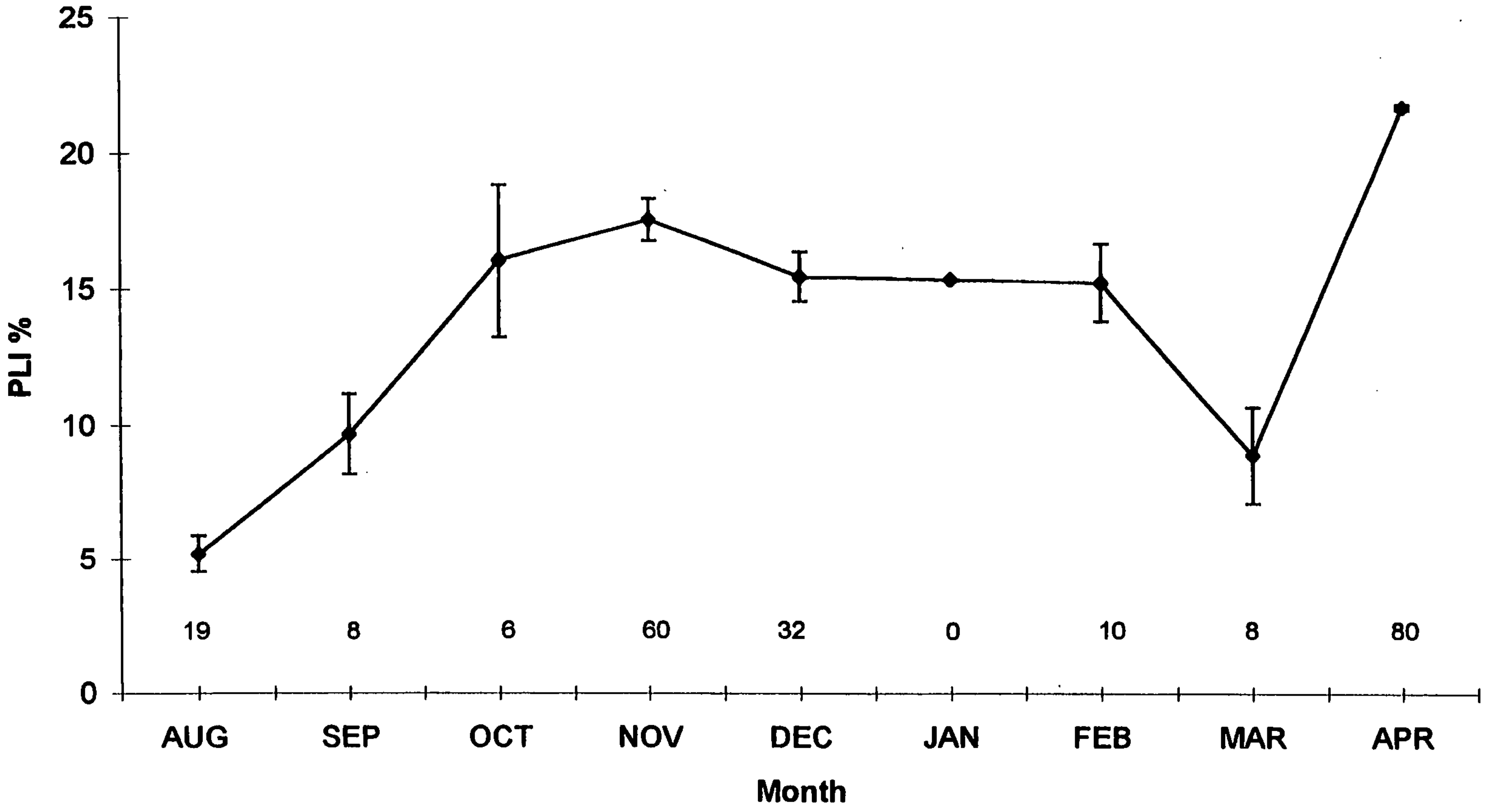


Figure 2.12: Predicted lipid index (PLI) of adult Redshank at Teesmouth 1992/93-94/95. Error bars indicate 2xSE. Numbers denote sample size.



PTLM was significantly greater in *robusta* than *britannica* (ANOVA $F_{1,197} = 6.519$ $P=0.011$) (Figure 2.13) due to differences in body size since PTLM′ did not vary significantly between races (ANOVA $F_{1,192} = 0.715$ $P > 0.05$) (Figure 2.14). In both races mean monthly PTLM′ was significantly greater in August and April than during mid-winter (ANOVA $F_{7,123} = 6.315$ $P < 0.0001$ for *robusta;* $F_{7,67} = 5.187$ $P = 0.0001$ for *britannica*; SNK $P < 0.05$). Likewise, PLI did not vary significantly between races (arcsine-transformed ANOVA $F_{1,195} = 0.223$ $P > 0.05$). Both races showed significant peaks (ANOVA $F_{7,69} = 6.842$ $P < 0.0001$ for *britannica;* $F_{8,126} = 9.061$ $P < 0.0001$ for *robusta;* SNK $P < 0.05$) in PLI in mid-winter, of 17% in *robusta* in December and 19% in *britannica* in November, and in April when mean PLI late in the month reached 25% in *robusta* and 23% in *britannica* (Figure 2.15).

Figures 2.16 and 2.17 show changes in PTLM and PLI respectively of 11 individuals caught and then recaptured at Teesmouth during the same non-breeding season (1992/93-1994/95). In general, individual changes in PTLM and PLI mirrored changes in the mean of the Teesmouth population (Figures 2.11-2.15). The changes in PTLM and PLI of 9 individual *robusta* paralleled the changes in monthly mean PTLM′ and PLI over the same period (Wilcoxon paired sample test $T_9 = 15$, $P > 0.05$ for PTLM; $T_9 = 6.5$, $P > 0.05$ for PLI; see section 2.3.3 for method of comparison used).

2.3.6 Comparison of body composition of wild and captive Redshank.

The seasonal variations in mean (Figure 2.18) and individual (Figure 2.19a-d) PLI and PTLM in the group of four captives kept between August and May paralleled

Figure 2.13: Predicted total lean mass (PTLM) of adult *robusta* and *britannica* at Teesmouth 1992/93-94/95. Error bars indicate 2xSE. Numbers denote sample size.

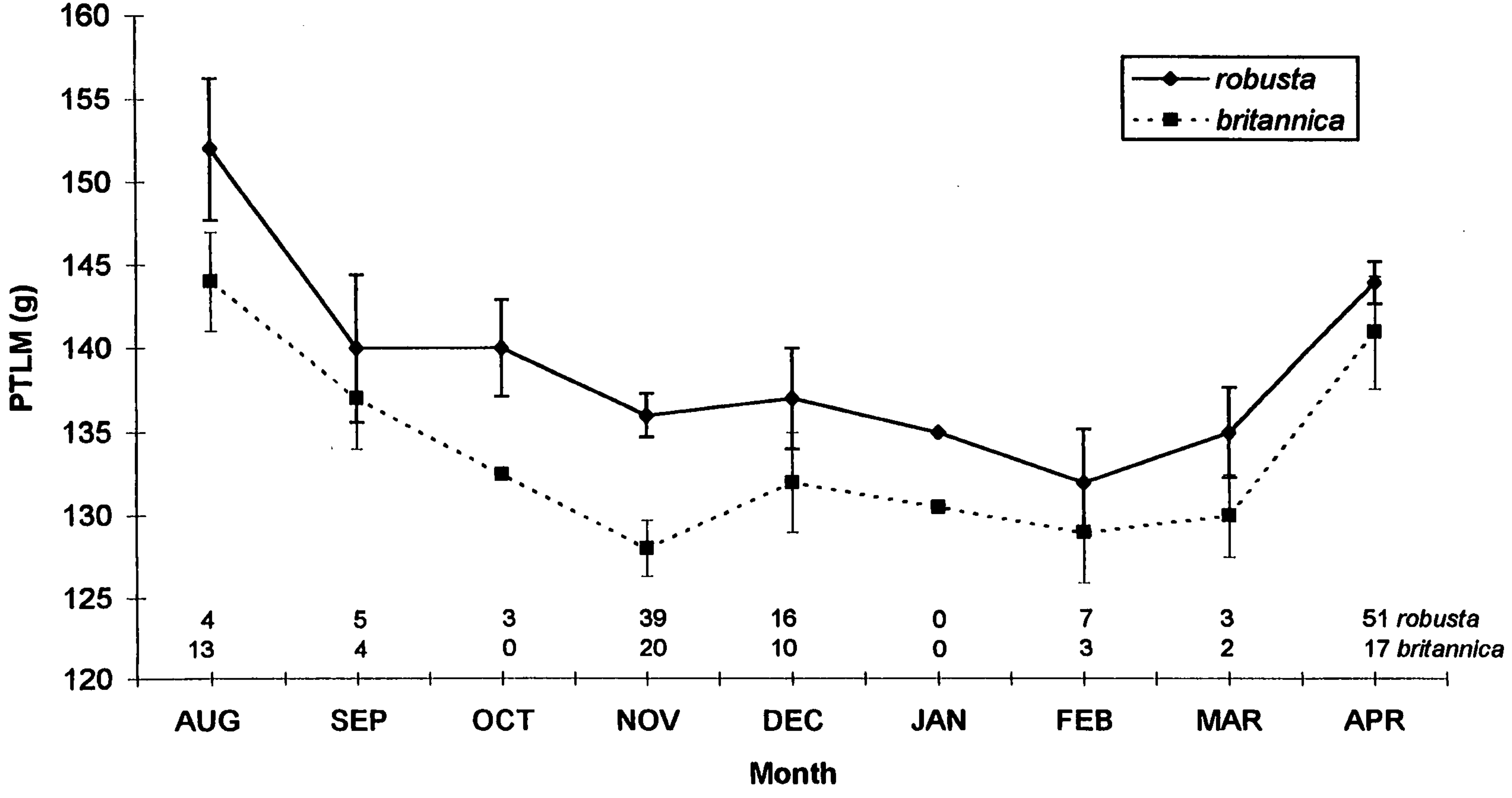


Figure 2.14: Size-adjusted predicted total lean mass (PTLM') of adult *robusta* and *britannica* at Teesmouth 1992/93-94/95. Error bars indicate 2xSE. Numbers denote sample size.

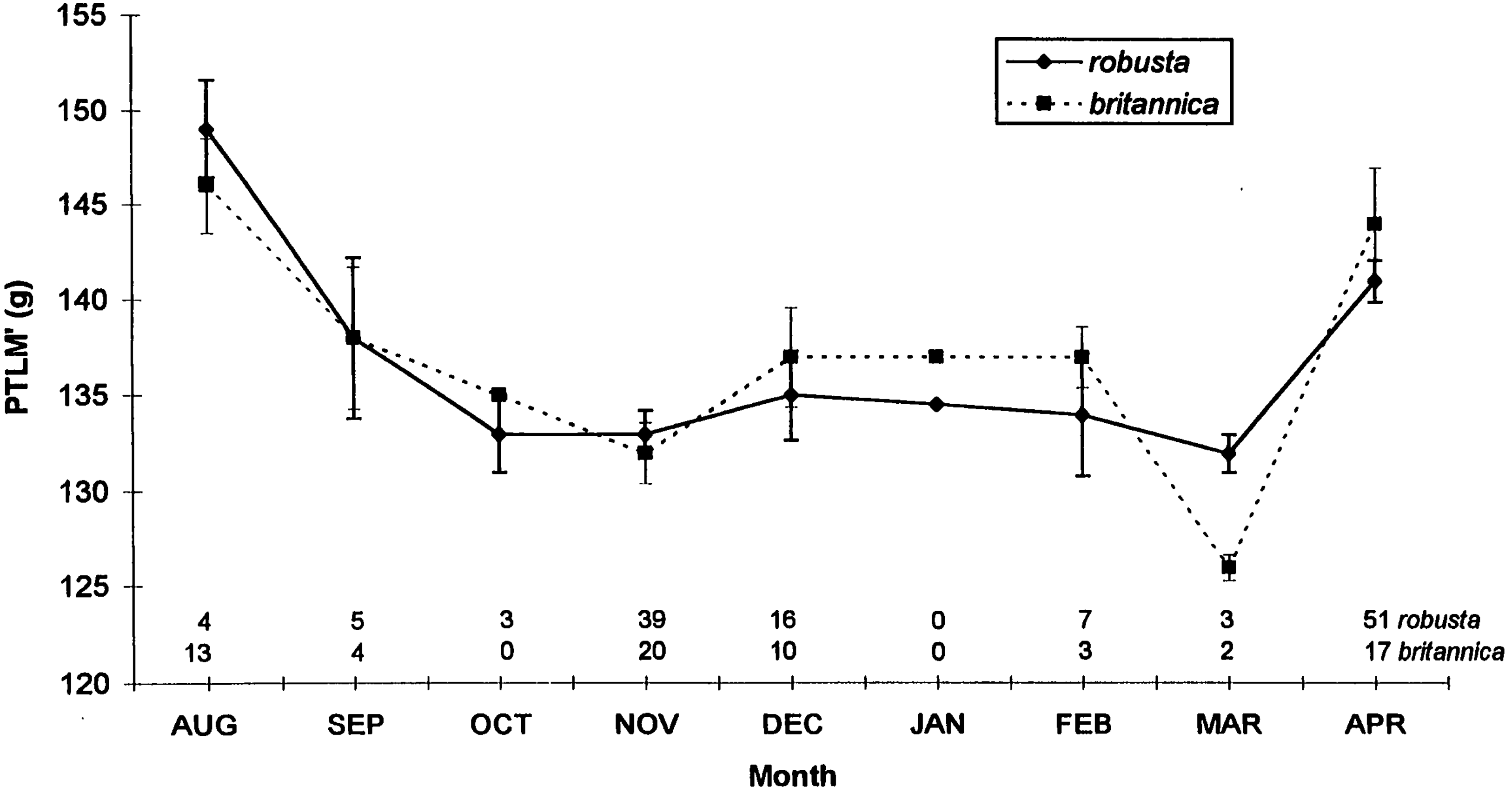


Figure 2.15: Predicted lipid index (PLI) of adult *robusta* and *britannica* at Teesmouth 1992/93-94/95. Error bars indicate 2xSE. Numbers denote sample size.

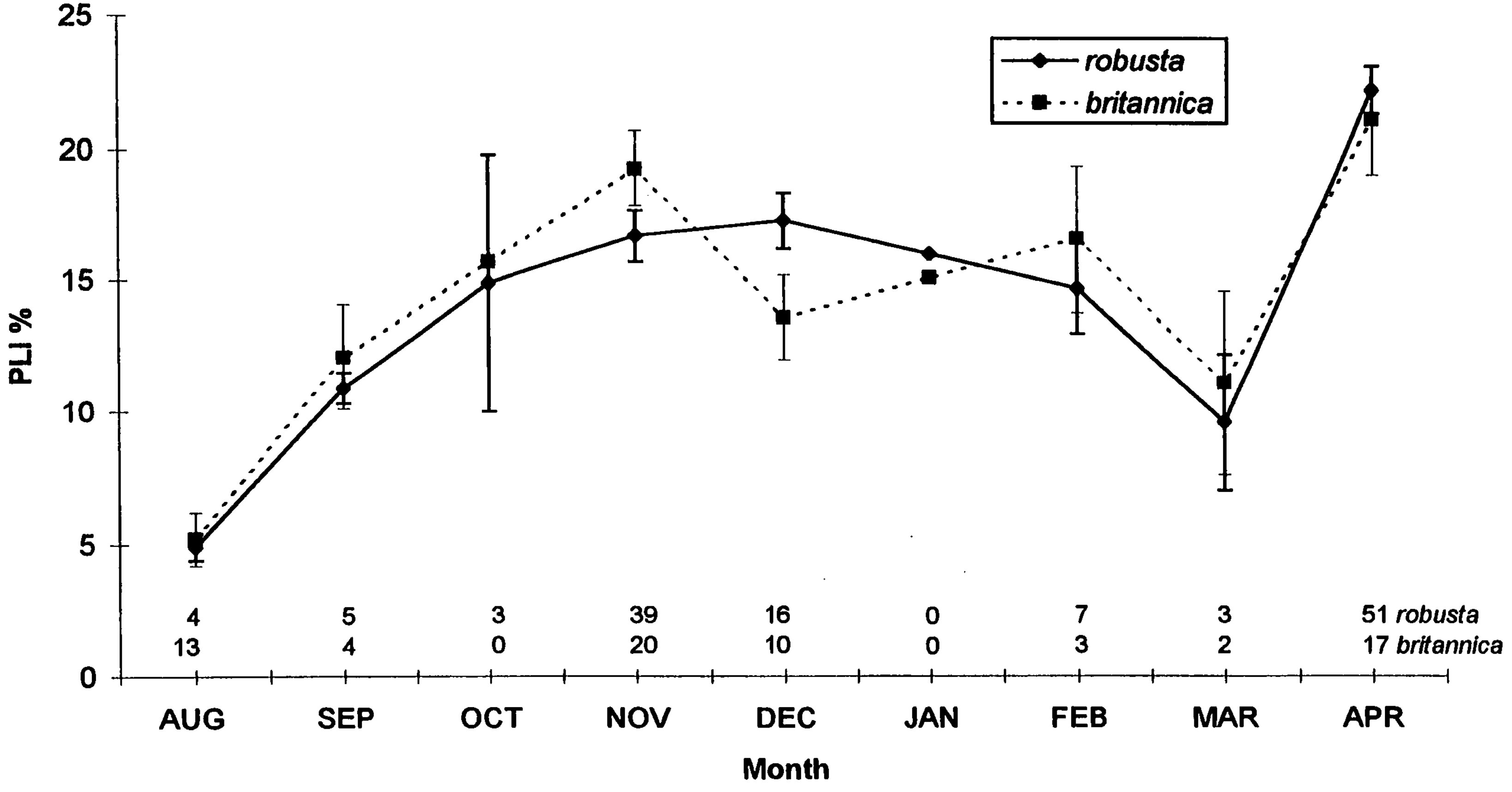
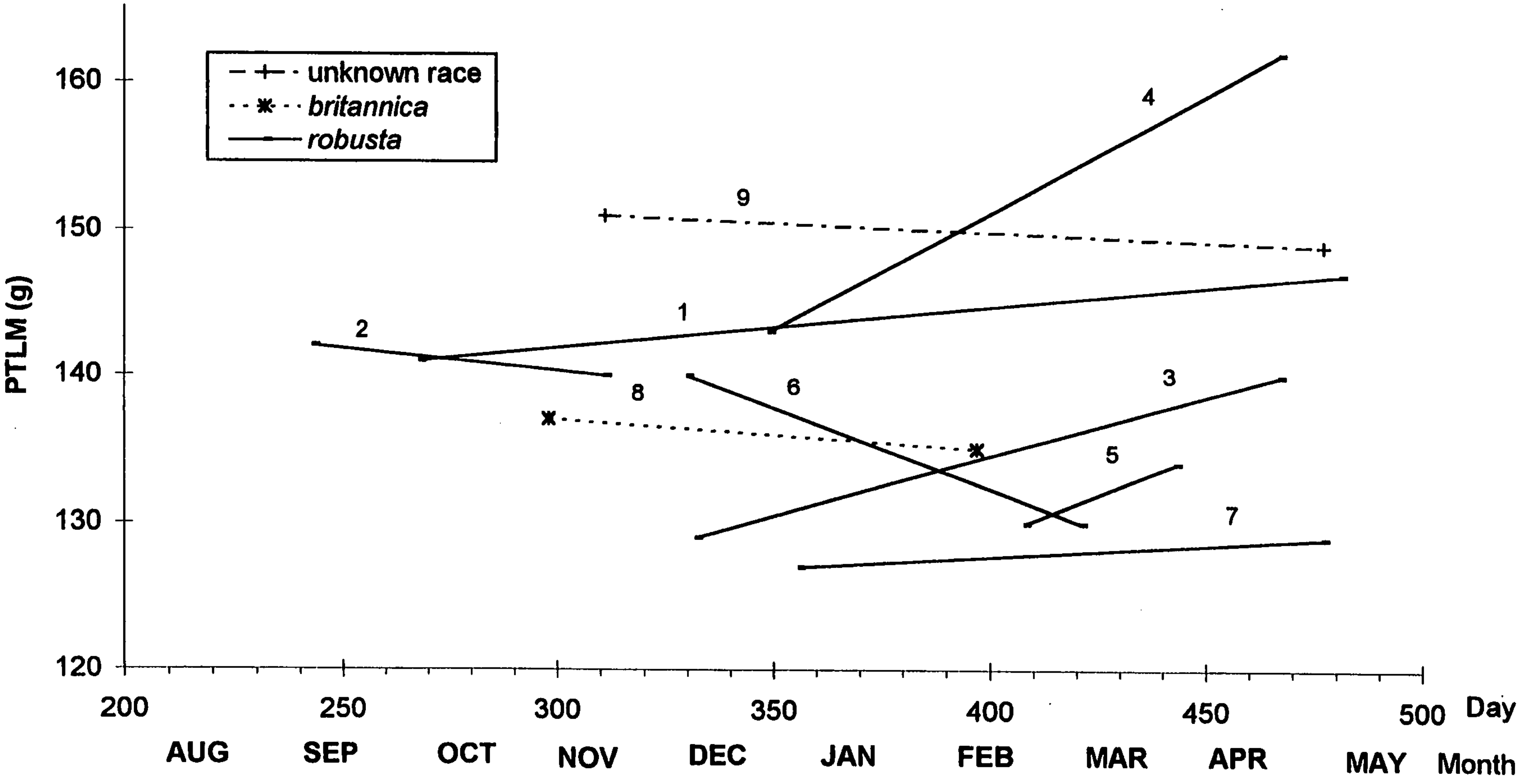
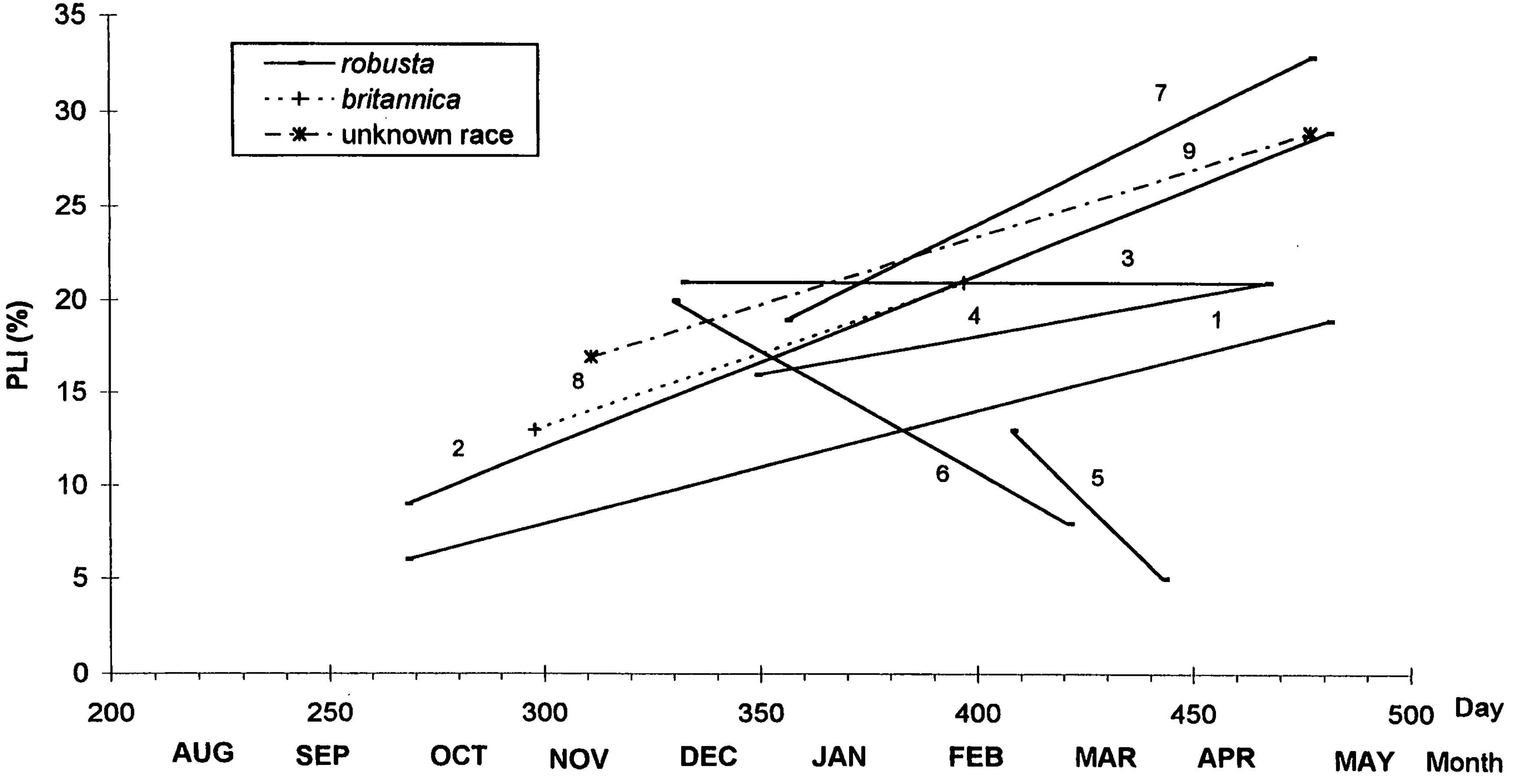


Figure 2.16: Changes in predicted total lean mass (PTLM) of individual Redshank recaptured at Teesmouth following capture earlier in the same non-breeding season (1992/93-1994/95).



Day 1= (e.g. 1992/93 season) on 1 Jan 1992 and Day=455 on 31 Mar 1993

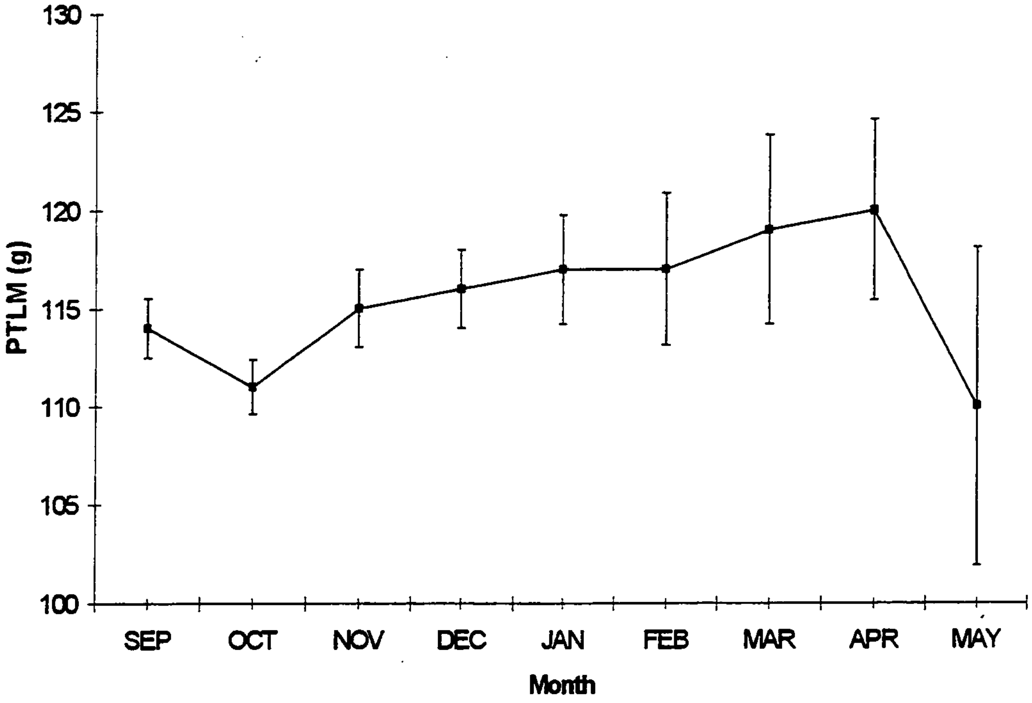
Figure 2.17: Changes in predicted lipid index (PLI) of individual Redshank recaptured at Teesmouth following capture earlier in the same non-breeding season (1992/93-1994/95). Numbers denote individuals.



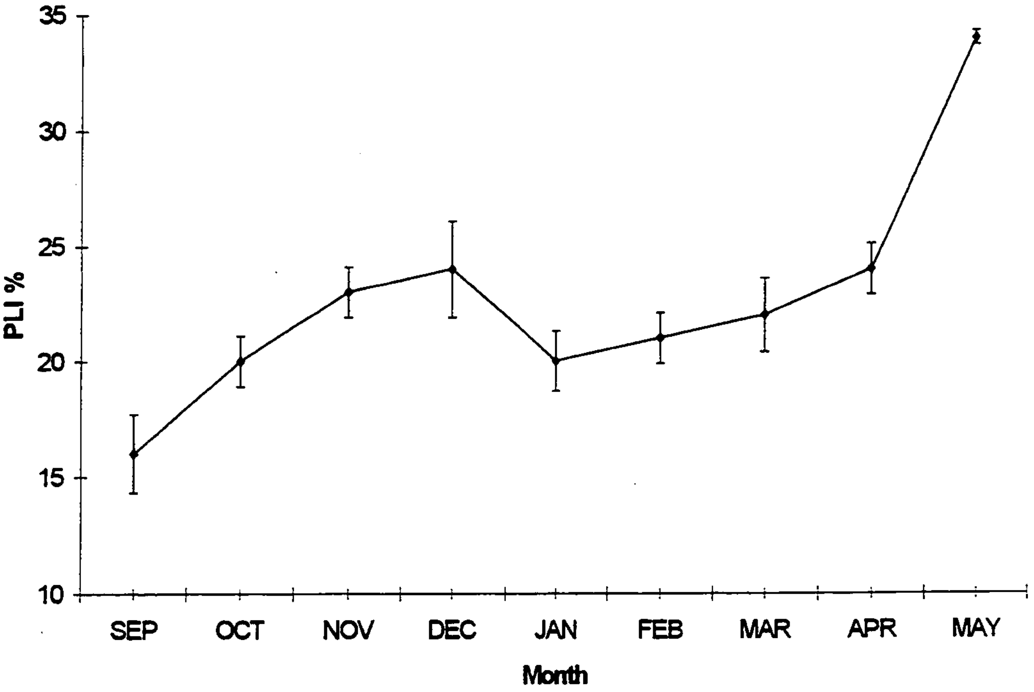
Day=1 (e.g. 1992/93 season) on 1 Jan 1992 and Day=455 on 31 Mar 1993.

Figure 2.18: Means of monthly mean a) predicted total lean mass (PTLM) and b) predicted lipid index (PLI) of four captive Redshank (individuals W, Y, R, and GW). Error bars denote 2xSE.

a) PTLM



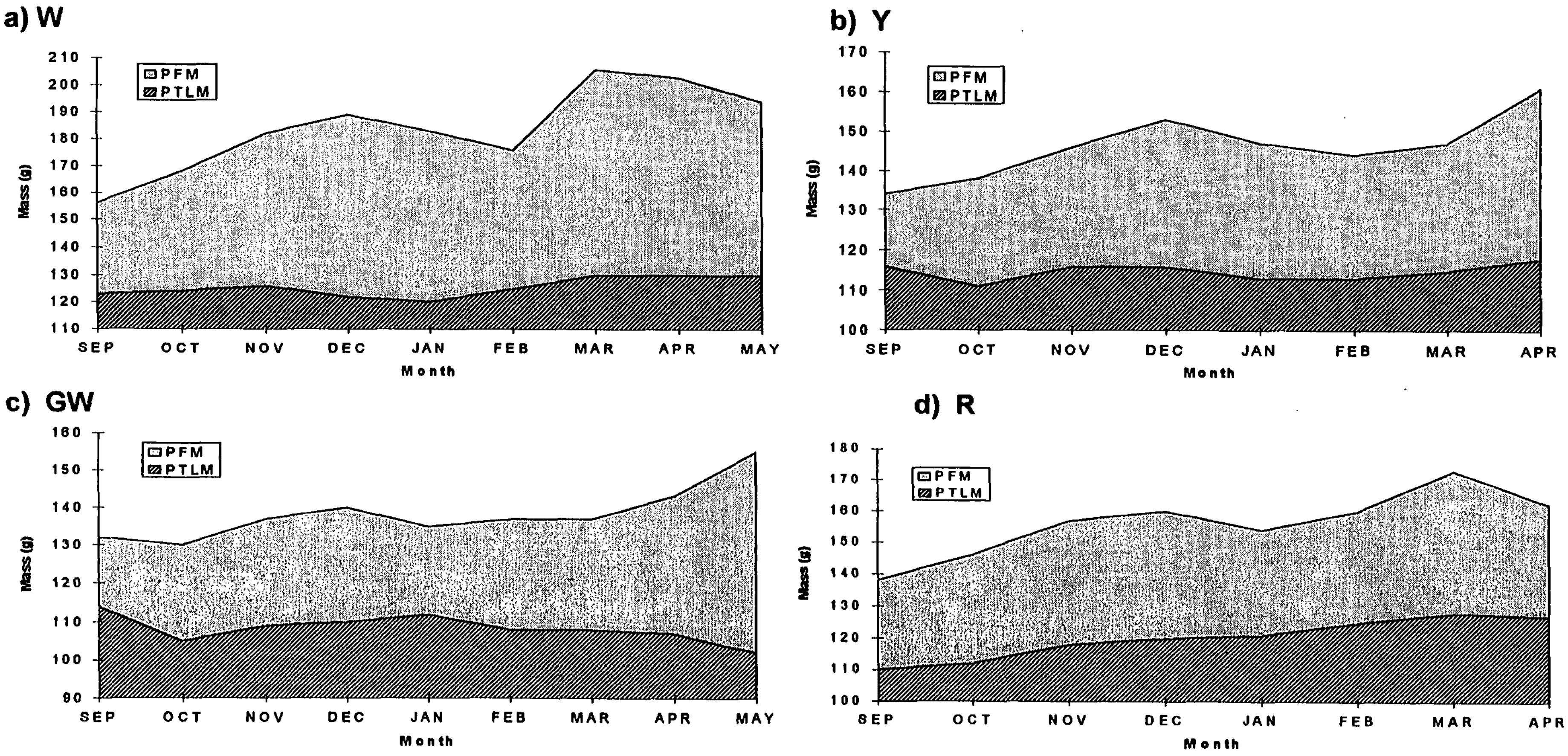
b) PLI



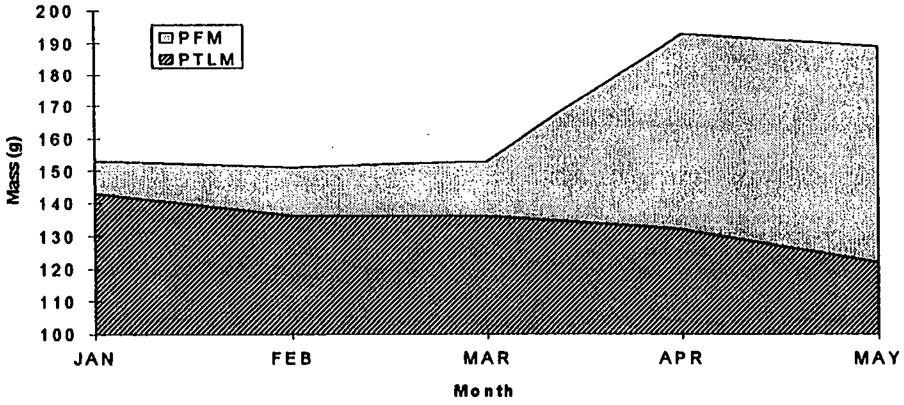
the changes seen in the wild population at Teesmouth. However the monthly mean PTLM of the captives was significantly less than the monthly mean PTLM′ of the wild birds (Paired T-test $t_6 = 15.194$ $P<0.001$), whereas the monthly mean PLI was significantly greater in the captives (Wilcoxon paired sample test $T_7 = 0$, $P < 0.01$).

PTLM of individuals L, N, RW, and G declined gradually whilst PLI increased following their entry into captivity (Figure 2.19e-h). In 16 Redshank which were brought into captivity at various times between October and March (1992/93-1994/95) PTLM (Figure 2.20b) had fallen significantly (Paired T-test $t_{15}=8.836$ $P < 0.001$) and PLI (Figure 2.20c) had risen significantly (T-test of arcsine transformed PLI $t_{15} = 4.113$ $P < 0.001$) after approximately 1 month in captivity. The changes in PTLM and PLI of an individual during its first month of captivity was different to the changes in PTLM and PLI occuring wild birds during the same period. The difference d_1 between an individual's PTLM and the wild mean PTLM′ at the time of capture was compared with the difference d_2 between an individual's PTLM and the wild mean PTLM′ 1 month later (see Scott*et al.*, 1994). d_2 was significantly less or more negative than d_1 (Wilcoxon paired sample test $T_{16} = 0$, $P < 0.001$), indicating that the 16 captive individuals had lost significantly more lean mass than their wild con-specifics over the same period. A similar analysis of the 16 individual captives' PLI and wild mean PLI showed that during their first month in captivity, the captive individuals had increased their mass of fat significantly more than their wild conspecifics over the same period (Wilcoxon paired sample test $T_{16} = 3$, $P < 0.001$). Conversely, the change in BM of the 16 captives during their first month of captivity (Figure 2.20a) paralleled changes in monthly mean BM′ of wild Redshank (Wilcoxon paired sample test $T_{16} = 43.5$, $P > 0.05$).

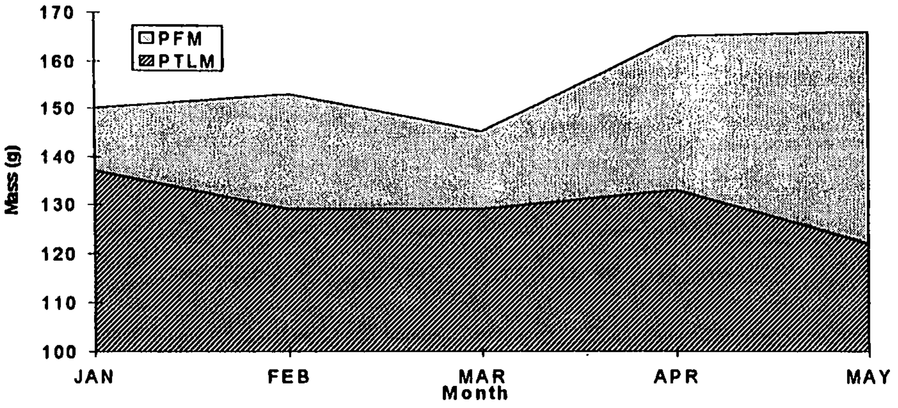
Figure 2.19: Mean monthly predicted total lean mass (PTLM) and predicted lipid mass (PFM) in individual captive Redshank.



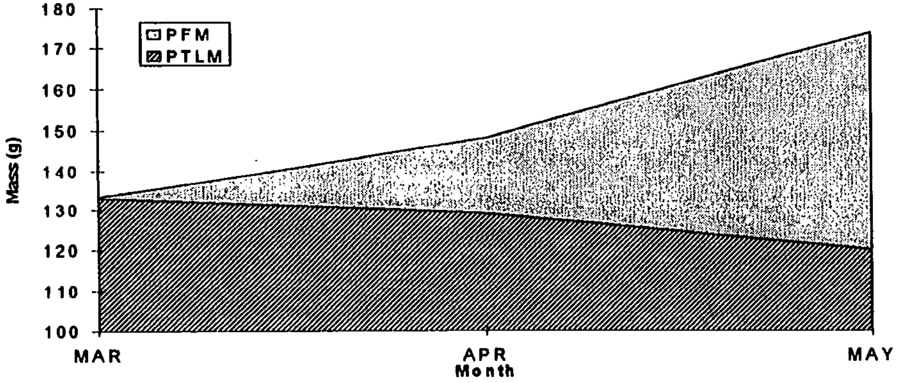
e) L


▨ PFM
▨ PTLM
Mass (g)
200
190
180
170
160
150
140
130
120
110
100
JAN
FEB
MAR
APR
MAY
Month

f) N


▨ PFM
▨ PTLM
Mass (g)
170
160
150
140
130
120
110
100
JAN
FEB
MAR
APR
MAY
Month

g) RW


▨ PFM
▨ PTLM
Mass (g)
180
170
160
150
140
130
120
110
100
MAR
APR
MAY
Month

h) G

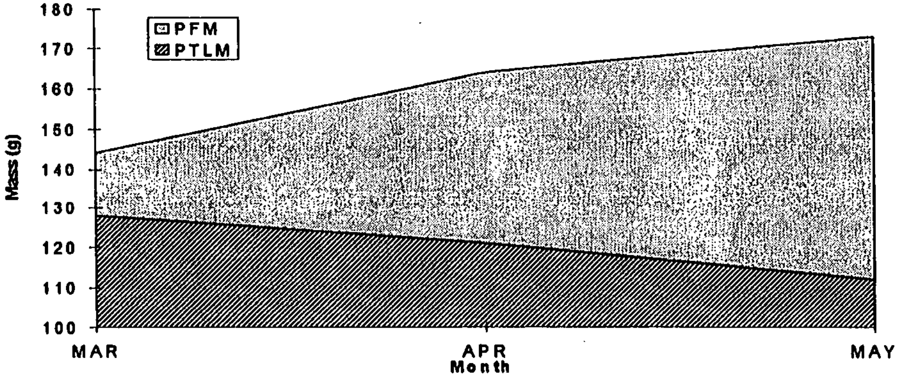
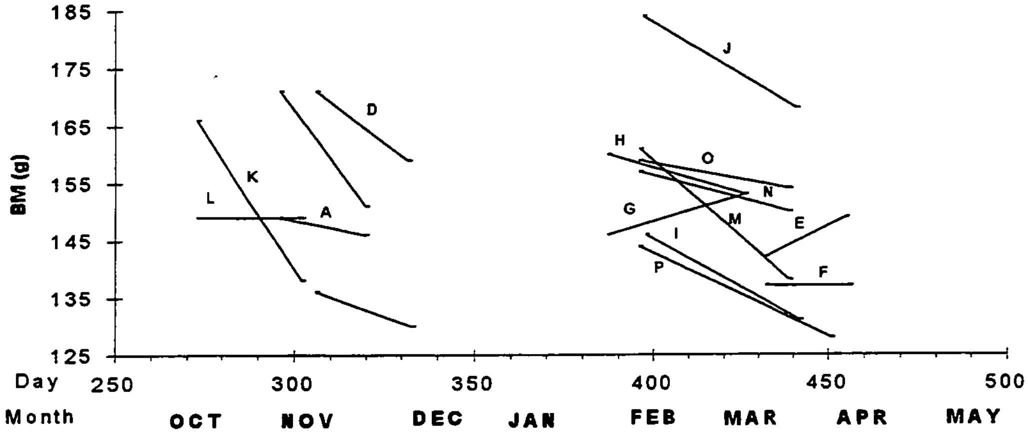
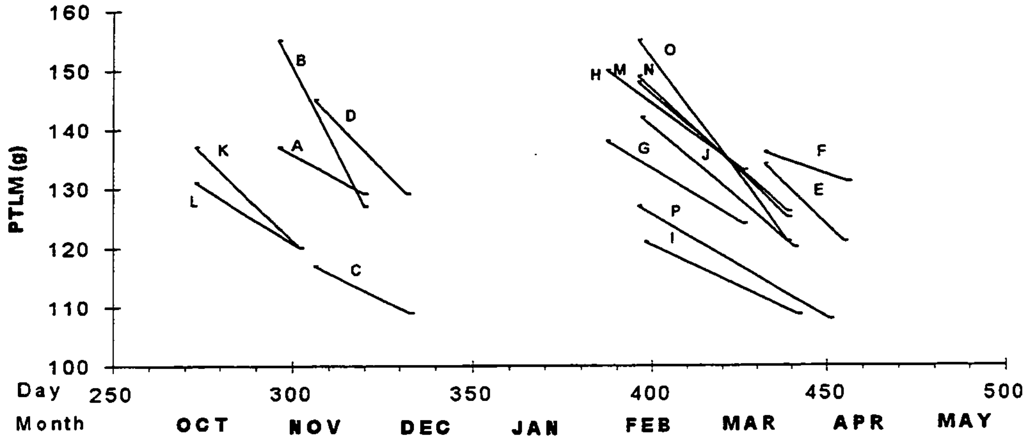

▨ PFM
▨ PTLM
Mass (g)
180
170
160
150
140
130
120
110
100
MAR
APR
MAY
Month

Figure 2.20: Changes in a) body mass (BM), b) predicted total lean mass (PTLM) and c) predicted lipid index (PLI) of individual Redshank after approximately 1 month in captivity following capture at Teesmouth. Letters identify individuals.

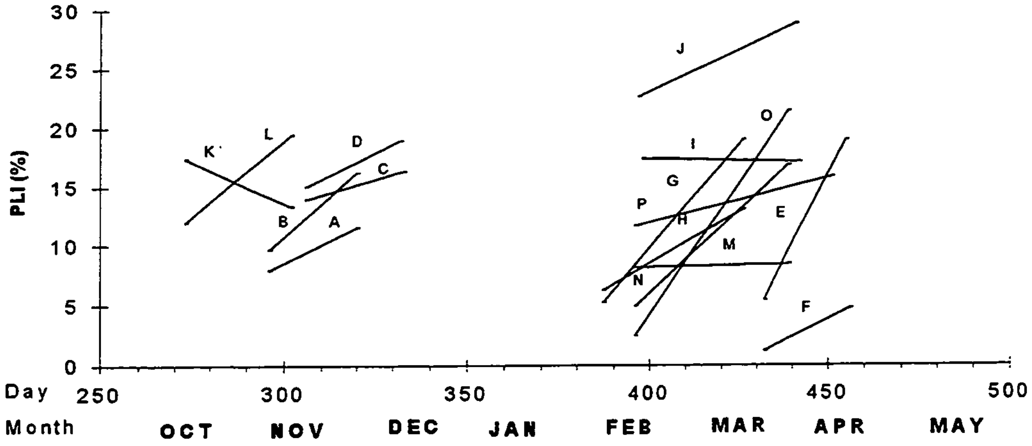
a) BM



b) PTLM



c) PLI



Day=274 on 1 October and Day=486 on 1 May.

Table 2.4: Comparison of organ size and mass in wild and captive Redshank. Values are means with standard errors in parentheses.

	captive (n=8)	wild (n=4)	t	level of P
fresh liver mass (g)	2.952 (0.238)	8.699 (1.469)	3.86	< 0.05
fresh pectoral muscle mass (g)	15.508 (0.997)	17.214 (0.358)	1.61	>0.05
†fresh standard muscle index	0.279 (0.0139)	0.3123 (0.0142)	*1.50	> 0.05
fresh stomach mass (g)	3.052 (0.232)	5.510 (0.625)	4.57	< 0.001
fresh intestine mass (g)	3.805 (0.916)	10.223 (2.685)	4.65	< 0.05
intestine length (mm)	583 (22.2)	909 (55.17)	6.644	<0.001
‡intestine thickness index	0.0066 (0.00057)	0.0111 (0.00095)	*4.11	< 0.01

* arcsine-transformed data used in test

† fresh mass of left pectoral muscle block / standard muscle volume

‡ fresh intestine mass / intestine length

The reduction in lean mass when birds entered captivity was attributable in part to a significant atrophy of the digestive system (see Table 2.4). Mean liver mass of 8 captives examined was one third of that in wild Redshank and mean stomach mass had halved. Mean mass of the intestine in the captives was less than half that of the wild birds, as a result not only of halving the length, but also of reducing the thickness. There was no significant difference in mean pectoral muscle mass between wild and captive Redshank.

2.4 Discussion

2.4.1 Body mass changes in wild Redshank during the non-breeding season

Significant seasonal changes occurred in BM of both adult and first year Redshank at Teesmouth. However, first year BM was consistently 10-15g lower than that of adults throughout the season and unlike adults, first years did not show a peak BM in mid-winter. The lower BM of first years could have been due to smaller body size, since first years had significantly shorter wings (ANOVA $F_{1,1392}$ = 180.4, $P<0.0001$). Additionally, the lower BM and lack of a mid-winter peak in BM of first years may have resulted from an inability to accumulate sufficient fat and protein stores because of less efficient feeding behaviour. Differences in foraging behaviour related to age have been shown in other species (e.g. on Blackbirds *Turdus merula* see Desrochers, 1992; for review see Marchetti & Price, 1989) but have yet to be demonstrated in Redshank. Body composition was determined in few first year Redshank which made comparisons with adult body composition inconclusive. However, the significantly lower BM of 5 first years (mean=135g SE=8.1g) compared to 6 adults (mean=164g SE=3.6g) caught on 25 October 1993 (T-test t_8=3.72, $P<0.01$) was in part, due to a significantly lower PLI in the first years (mean = 4.7% SE=2.07 for first years; mean=16.1% SE=2.76 for adults, T-test t_8=2.83, $P<0.05$). For the same sample, PTLM of the first years (126g SE=5.2g) was lower than that of the adults (137.3g SE=2.8g; T-test t_8=2.13, $P=0.065$), though this may have resulted from the larger body size of the latter.

The mid-winter peak of 165g (the mean BM of all adult Redshank at Teesmouth irrespective of race) was comparable with findings of other studies on east coast estuaries, 164g (n=399) in the Moray Basin (Swann & Etheridge, 1989) and 166g (n=187) on the Wash (Johnson, 1985). Furness & Baillie (1981) suggested that in October and November, the proportions of *britannica* and *robusta* on 11 British east coast sites (including Findhorn in the Moray Basin and The Wash) might be similar which could account for the similarity in mid-winter peak BM in Redshank at Teesmouth, the Moray Basin and the Wash. However, the increase in mean BM (compared to September levels) at Teesmouth of 8.6% was lower than the 12.3% found in the Moray Basin and 13.6% on the Wash, attributable to lower mean BMs in September of 146g and 147g respectively compared to 152g at Teesmouth. This difference may have been due to a greater proportion of the smaller *britannica* being present in Autumn in the Moray Basin and the Wash than at Teesmouth. Certainly at Teesmouth, *britannica* are more numerous in August and September than in mid-winter when *robusta* predominated.

The effect of seasonal changes in proportions of the two races on the mean BM of birds at a given site should be taken account of when comparing seasonal body mass changes between sites. In my study I adjusted the BM of each individual to that of a bird of a standard body size. In doing so, the means in September when *britannica* predominated increased but in mid-winter when *robusta* was more numerous decreased, thus reducing the mid-winter increase to just 5.2%. The decline in BM from December to March of 9.7% was little affected by biases in body size (8.6% decline in BM′). Declines of 10.3% were recorded in the Moray Basin Redshank (Swann & Etheridge, 1989) and 13.8% on the Wash (Johnson, 1985).

Adjusting for body size was used to demonstrate that *robusta* and *britannica* showed identical seasonal changes in BM relative to body size, despite *robusta* being significantly heavier. The only difference in the patterns of BM change was that *robusta* showed a peak in mean BM in November whilst *britannica* peaked in

December. The slight rise in mean BM of *robusta* during February was possibly due to sample bias since all the birds in the sample were caught in the first two weeks of February 1994. The unexpectedly high BM could have been a proximate response to short-term weather conditions as observed by Swann & Etheridge (1989).

Surprisingly both races exhibited large increases in BM during April. Pre-migratory increases would be expected in *robusta* which were about to embark on a 1600km flight to breeding grounds in Iceland, but not in *britannica* which are usually thought to move no more than 300km from their breeding site (Hale, 1973). However, this increase in BM of *britannica* is not a result of larger sized birds arriving at Teesmouth since similar increases were shown in mean BM′ and increases similar to the mean BM change were shown in 13 individuals (including 3 *britannica*) which were recaptured in April after being caught earlier during the same winter. It might be argued that the birds identified as *britannica* were in fact *robusta* since most British-breeding Redshank should be on the breeding grounds by April. However, identifying race using the discriminate function of Summers *et al.* (1988) with a 0.7 probability threshold (Appendix I) would not account for 21 out of 105 Redshank caught in April being identified as *britannica*. Alternatively it could be that the age of the "*britannica*" in April could have been mis-identified since age determination in Redshank becomes progressively more difficult throughout the non-breeding season, as juvenile contour feathers are gradually replaced by adult plumage. If this was so, the birds identified as adult *britannica* could in fact have been first year *robusta* which would have shorter wings than adults and therefore, greater chance of being mis-identified as *britannica*. However, the 3 *britannica* which were recaptured in April had been aged as adults in the previous August (2 birds) and November when the determination of age in Redshank is not a problem. Additionally, a further 2 *britannica* caught in April had been caught in previous years and were therefore definitely adults.

Given the levels of fat accumulated by both races at Teesmouth in late April and early May, I used the model of Castro & Myers (1989) to predict that the potential flight ranges of *robusta* and *britannica* (flying at an airspeed of 65km/h) would be 2,285km and 2,026km respectively. Hence, even the birds identified in late April as *britannica,* are potentially capable of migrating to Iceland in a single flight. However, if these *'britannica'* did migrate to Iceland, they would have very low fat reserves, an LI of 2.1% compared to 5.3% in *robusta* which made the same journey.

Alternatively, the heavy *britannica* at Teesmouth in April could be from breeding sites in northern Scotland, possibly even as far north as Shetland which would require around a 600km flight over water directly from Teesmouth. Castro & Myers' (1989) model would predict that *britannica* leaving Teesmouth would arrive in Shetland after a non-stop flight with a LI of 12.7%. This substantial fat reserve on arrival on the Shetland breeding grounds may be advantageous in the harsh climate which would also account for the later departure of these birds compared with more locally breeding Redshank.

There has yet been no ringing recoveries of these heavy *britannica* from either Iceland or Shetland to prove or dispute the possibilities that these birds are northerly breeding *britannica*, perhaps headed for Shetland, or are infact *robusta* which migrate to Iceland.

2.4.2 Control of body mass in Redshank

The significant correlation between the seasonal changes in BM′ of wild Redshank and those of captive Redshank given unlimited food demonstrates clearly that Redshank at Teesmouth have a preprogrammed seasonal pattern of variation in body mass. Since the main environmental variant in captivity was daylength, it is highly likely that this controls the timing of seasonal body mass change in the wild, either directly or by synchronizing an endogenous circannual clock. The fact that the captive birds were lighter during mid-winter than in Spring even when excess food was provided shows that they were maintaining optimum rather than maximum body mass during mid-winter. This demonstrates a trade-off between the advantages of carrying enough energy stores to provide for periods of negative energy balance and the costs of being heavy (Lima, 1986; Witter & Cuthill, 1993) in terms of greater energy expenditure for maintenance and locomotion as an individual increases in mass (Scott, 1991; Scott *et al.*, 1996) and increased risk of predation (Gosler *et al.*, 1995). On some estuaries Redshank populations can suffer substantial losses to avian predators (Cresswell & Whitfield, 1994). Increasing mass has been shown to reduce manoeuvrability in flight in Starlings (*Sturnus vulgaris*) (Witter, Cuthill & Bonser, 1994) and Great tits (*Parus major*) have been shown to maintain lower body masses when predation risk is high (Gosler *et al.*, 1995).

Food supply did not limit body mass gain in the wild before mid-winter as suggested by some authors (Owen & Cook, 1977; Maron & Myers, 1985) since the mid-winter peak BM was no less in wild Redshank than in captivity where food was provided *ad libitum*. Furthermore, the rate of decline in BM was similar in both wild and captive Redshank, refuting Davidson's (1982a) conclusions that Redshank on the east coast of Britain were unable to regulate body mass in late winter. Davidson's conclusions were based on the fact that peak mid-winter mean and February BM of Redshank populations on east coast Britain were lower than expected from a regression of mean BM against mean air temperature at sites on the west and south coasts of Britain. Davidson's findings may have been confounded by the fact that south coast populations hold greater proportion of *britannica* than on the east coast (Furness & Baillie, 1981). Therefore, warmer sites on the south coast will have lower mean BM as a result of a higher proportion of *britannica* compared to east coast sites and not necessarily as a result of south coast birds maintaing a low mid-winter peak BM in response to the warmer conditions. Consequently, mean BM′ of Redshank at warmer south coast sites may infact be similar to the mean BM′ of those at colder east coast sites.

2.4.3 Body composition changes in Redshank during the non-breeding season

Both races of Redshank at Teesmouth underwent similar seasonal changes in lean mass and lipid reserves, accumulating the same amounts of fat stores in mid-winter in relation to body size. Peak mid-winter mean PLI of around 18% was higher than the 13% recorded in Redshank at Teesmouth by Davidson (1982a), though his sample size was very small. In PTLM there was no detectable decline during the second half of winter which might have resulted from the atrophy of pectoral muscles (Davidson, 1982a). Sample sizes analysed for body composition in my study were small between January and March since Redshank at Teesmouth became difficult to catch at this time of year since they changed roost sites; those they used then were mostly inaccessible.

The significant peaks in PTLM during August and April in captive and wild *robusta* and *britannica* could have been due to hypertrophy of the gut to aid digestion to allow faster fattening, or of the pectoral muscles to aid migratory flight (Davidson & Evans, 1990; Evans *et al.*, 1992; Piersma, 1990) from and to the breeding grounds respectively. Alternatively, total blood volume may have increased during primary moult to provide additional blood supply to the tracts of growing feathers, as found in Bullfinches (*Pyrrhula pyrrhula*) (Newton, 1968). An increase in blood volume would in effect, cause an increase in TLM even though no increase in the mass of lean tissue had taken place. Using TOBEC to monitor changes in PTLM which involve changes in blood volume may have a potential problem: the curve used to predict TLM from TOBEC indices (see Appendix II) was based on the effect of changes in the lean mass of tissues on TOBEC; the effect of changes in blood volume on TOBEC may be different. Further study is obviously required to investigate the validity of using equations derived from TOBEC measurements and carcass analysis of non-moulting birds, to determine PTLM in birds undergoing primary moult

The comparison of organ masses of wild and captive Redshank demonstrated that Redshank are capable of significantly reducing mass of tissue in the alimentary canal and the liver. The reduction in size of the stomach of captive Redshank compared to those in the wild may be a response to the change in diet to softer food items (i.e. trout-pellets and blow-fly larvae) in captivity. Piersma *et al.* (1993) demonstrated that Knot which were fed on trout-pellets in captivity had smaller, and thinner-walled stomachs than their wild conspecifics which fed predominantly on whole bivalve molluscs. The wild Knot required more muscular stomachs to be able to break-up the shells of the molluscs. Similarly, wild Redshank feed on harder, less easily digestible prey than those provided in captivity. For example, such as the small amphipod crustacean *Corophium volutator* which has a chitinous exoskeleton, and the small gastropod mollusc *Hydrobia ulvae,* both being swallowed whole (Goss-Custard & Jones, 1976; Goss-Custard *et al.*, 1977; Evans *et al.*, 1977). Piersma *et al.*(1993) also inferred that increased absorption of softer prey by the stomach, may reduce the amount of absorption performed by the intestine which would explain the shortening and thinning of the intestine of captive Redshank in my study.

The reduction in liver mass during the first few weeks of captivity may have been a response to a reduction in total energy expenditure resulting from lower levels of activity and lower maintenance costs in indoor aviaries. The lower rate of energy expenditure in captivity would require less rapid turnover of glycogen and possibly protein by the livers of captive birds than their wild conspecifics. It appears therefore, that the Redshank in my study reduced the rate of glycogen and protein turnover by reducing liver mass. Captive Knot have also shown a similar reduction in liver mass (Piersma *et al.*, 1996; C. Selman unpubl. data). Piersma *et al.* (1996) interpreted this ability to vary the mass of certain organs as an adaptation to the highly variable metabolic demands of migratory shorebirds.

2.4.4 The control of fat and protein reserves

Redshank which were brought into captivity appear to compensate for the reductions in lean mass which occur as a result of atrophy of the gut and liver by accumulating proportionally more fat than conspecifics in the wild. It appears then, that Redshank are regulating total body mass at set levels throughout the year. It could be concluded that Redshank weigh themselves. The necessity to achieve high and possibly pre-set levels of body mass before departure on migration was shown in Knot (Evans, 1992) at the Balsfjiord staging post in Norway; Knot which delayed departure from the staging post to the breeding grounds were significantly lighter than those which left.

3.0: Energy Expenditure

3.1 Introduction

In the previous chapter it was shown that both races of Redshank wintering in Britain accumulate similar mass-specific levels of fat and protein reserves in winter and both races are equally capable of regulating these levels. It could be argued therefore, that both races are equally prepared in nutritional terms for the energetic demands of the British winter. This would be a fair assumption if both races had the same mass-specific energy demands during winter. Section 1.4 however, outlined several reasons why the mass-specific rate of energy expenditure in *britannica* and *robusta* may not necessarily be the same. Therefore, the aims of this chapter are to determine firstly, whether basal metabolic rate is similar in both races; secondly, whether the rates of heat loss and metabolic heat production in response to cold is similar in both races; and thirdly, how energy expenditure in both races under standard conditions translates into energy expenditure in the field.

In this chapter measurements of Standard Metabolic Rate (SMR) and of Standard Operative Temperature (T_{es}) (see below) obtained using taxidermic mounts are combined to estimate maintenance metabolism (M_{maint}) of both *britannica* and *robusta* that would have been experienced during those periods of severe weather in the last 20 years. Such periods of severe weather have given rise to large scale mortality amongst wintering Redshank populations in Britain. I will determine whether M_{maint} of the two races is similar during such periods or whether one race has a greater risk of mortality due to higher M_{maint}. By comparing estimated levels of M_{maint} experienced during periods which were associated with Redshank mortality and those that were not, I will determine which weather conditions are most likely to cause significant mortality.

3.1.1 Levels of energy expenditure in birds

Piersma *et al.* (1991) and Piersma & Morrison (1994) suggested that the majority of variation in daily energy expenditure (DEE) of free-living birds is attributable to variation in maintenance metabolism (M_{maint}), which is '*BMR plus extra costs for thermoregulation at environmental temperatures below the thermoneutral zone*' (Wiersma & Piersma, 1994). The amount of heat required to maintain body temperature is determined by the thermal conductance of the animal which is "*a measure of the ease of heat transfer from the body by radiation, conduction, convection and evaporation and is the reciprocal of insulation*" (Bradley & Deavers, 1980). The rate of heat loss is a result of the combined effect of the thermal conductivity of the skin and plumage and the temperature gradient between the core of the animal and the ambient environment.

In the field, heat loss is influenced by the combined effect of air temperature and wind speed. Whilst the effect of wind speed and temperature as lone variants is well understood (Scholander *et al.*, 1950; Bakken, 1976; McArthur, 1991; Bakken & Lee, 1992) it is much more difficult to quantify their combined effect on heat loss (Bakken, 1990; Bakken *et al.*, 1991). Standard Operative Temperature T_{es} is an 'environmental temperature' which combines the effects of air temperature, wind speed and solar radiation (Bakken, 1980). T_{es} and hence M_{maint} can be measured directly using heated taxidermic mounts (Bakken *et al.*, 1981; Wiersma & Piersma, 1994). Each consists of a copper core which is heated to body temperature T_b and covered by the intact skin and feathers of the species under study. Thus, the energy required to maintain the mount at T_b is proportional to the T_{es} experienced by the bird under field conditions. The M_{maint} predicted by the heated mount method is the energy value which must be met by the bird in addition to any cost of activity. M_{maint} may be attained not only by assimilation of food; both the heat increment of feeding and thermogenesis from muscles during activity may also contribute to M_{maint}.

The maximum sustained rate of energy expenditure (for M_{maint} and activity combined) of birds not on a migratory flight was thought to be 4 times BMR (Drent & Daan, 1980). Bryant & Tatner (1990) questioned that all taxonomic groups of birds have a maximum sustainable level of 4 times BMR, since they found some passerines could sustain levels up to around 6 times BMR. Bryant & Tatner (1990) found that sustained energy expenditure levels above 4 times BMR were associated with species which have an energetically expensive mode of foraging (e.g. Pied Kingfisher (*Ceryle rudis*), Dipper (*Cinclus cinclus*), Swallows and Martins (*Hirundinae*)). However several studies have found a maximum sustainable level of around 4 times BMR to exist in shorebirds (Piersma *et al.*, 1991; Piersma & Morrison, 1994; Poot & Piersma, in Piersma, 1994).

3.1.2 Energy expenditure in shorebirds during severe weather

The energy expended by shorebirds during those periods of severe weather which significantly increase mortality rates has never been quantified. It is unclear from the literature what combination of weather conditions are most likely to cause large scale mortality. Most reports refer to 'very low' temperatures and 'prolonged freezing' (e.g. Jourdain & Witherby, 1918a&b; Ticehurst & Hartley, 1948; Dobinson & Richards, 1964; Davidson & Clark, 1985b). However, it is unclear exactly how low temperatures must fall and for how long before birds start to die as a result of either starvation from an energy debt, or an inability to produce heat fast enough. Most reports are isolated and confined to a particularly severe year. They rarely compare conditions during severe periods which have resulted in mortality and during periods which could be considered severe but did not significantly raise mortality .

For conservation purposes, the British Wildlife and Countryside Act 1981 defines 'severe weather' on a national basis (i.e. Great Britain) when more than half of 26 designated coastal stations report frozen ground (see Batten & Swift, 1982;

Stroud, 1992). However, severe weather resulting in mortality is often localised and therefore severity on a national scale may not necessarily be indicative of potentially lethal conditions at a single site.

Dugan *et al.* (1981) highlight the potential importance of strong winds in interrupting food intake in some species, especially Grey Plover (*Pluvialis squatarola*). They and Beecroft & Clark (1986) also considered the effect of wind on heat loss and hence energy expenditure. The use of heated mounts in this study for estimating T_{es} allows determination of the importance of wind speed as a factor in causing large scale mortality in Redshank.

Kirby (1995) is the only study in which energy expenditure rather than low temperatures or freezing ground has been used to define the severity of conditions. He used the model of Wiersma & Piersma (1994) to estimate M_{maint} for Knot. By examining regional and national weather data he identified certain periods of weather as severe on a regional or national level, namely those during which M_{maint} exceeded 3.5xBMR, the supposed sustainable limit in Knot (Piersma *et al.*, 1991).

The definition of severity of weather based on energy expenditure of Knot (Kirby, 1995) may not necessarily be an appropriate 'bench-mark' to apply to other shorebird species, since Knot do not suffer losses during severe weather as high as some other species. In addition, Knot are "plump" in shape for their size and do not have long legs and therefore, may not experience such strong windspeeds as longer-legged shorebirds. Redshank, however, consistently suffer the highest rates of mortality during severe weather (see chapter 1). Therefore, a bench-mark level of weather severity based on the conditions which lead to a lethal energy debt in Redshank, will be more applicable to estimating the risk of mortality of all shorebird species during severe weather.

3.1.3 Estimation of M_{maint} and T_{es} during past severe winters

In order to determine what weather conditions and what levels of energy expenditure (in terms of M_{maint}) lead to increased mortality in Redshank, it was necessary to compare periods of high mortality with those where weather had no apparent effect. Some reports of mortality during winter are based on recoveries of dead ringed birds, but more frequently arise from shoreline searches for carcasses. Unfortunately estimates of mortality rates from shoreline searches are subject to biases from searching effort, which tends to be greater when the perceived chance of mortality amongst shorebirds is greater (i.e. during periods of perceived severe weather). Therefore it is difficult to ascertain whether low numbers of recovered carcasses do in fact reflect low mortality or just a low search effort. Aware of this problem, the Wader Study Group (WSG) carried out an investigation on the effects of severe weather on waders during the winters of 1982/3-1985/86 (Davidson & Clark, 1982,1983a&b, 1984, 1985a&b; Clark & Davidson, 1986). The project consisted of systematic carcass searches around the coasts of Britain. There were periods in the winters of 1984/85 and 1985/86 during which mortality was higher than in the previous two winters (Clark & Davidson, 1986; Davidson & Clark, 1985b). It became clear during the study that lethal conditions and resultant mortality were localised. Mortality during 'severe' periods in south-east England was not always accompanied by notable mortality at Teesmouth in north-east England. Hence weather conditions and estimates of M_{maint} were compared between Teesmouth and the Wash (Lincolnshire/Norfolk).

Additional comparisons were made for winters during which elevated mortality amongst Redshank (and other shorebirds) had been reported in detail in the literature (see below).

3.1.4 Background: a summary of Redshank mortality at Teesmouth and the Wash

In January and February 1979 conditions were considered severe enough to impose a ban on wildfowling (Batten & Swift, 1982), though large-scale mortality of Redshank appeared to be restricted to Eastern Scotland (Baillie, 1980). "Few" corpses were found at Teesmouth (Davidson, 1982b), but ringing recoveries suggested an increase in mortality during these two severe months (Davidson, 1982c). There is no record of large-scale mortality of Redshank on the Wash during the 1978/79 winter.

Severe weather in December 1981 and January 1982 led to wildfowling bans in England from 22 December 1981 until 5 January 1982 and again from 13-25 January 1982 (Evans, 1982; Stroud, 1992). A total of 99 Redshank corpses was reported from the Wash between 23 December and 5 January (Clark, 1982). Searches were sporadic and covered only 1.6km of the north-west shore and 7km of the east shore, and so the total number of Redshank which may have died could have represented a substantial proportion of the 2-3000 which are normally present in mid-winter. Only 2 Redshank corpses were recovered at Teesmouth (Clark, 1982), though ringing recoveries of birds ringed at Teesmouth suggested an increase in mortality of Redshank during December 1981 and January 1982 compared with the previous two winters (Davidson, 1982c).

The WSG survey recorded only 3 Redshank corpses during 1982/83 winter (Davidson & Clark, 1983b) and 26 during 1983/84 (Davidson & Clark, 1984) along 80-100km of coastline throughout Britain. In contrast, much larger numbers of corpses were recovered during the two subsequent winters. In January 1985 prolonged freezing and snow cover led to a wildfowling ban being imposed in England from 16-29 January. There then followed a second period of severe weather in February when more corpses were recovered than during January. In total around 240 Redshank corpses were recovered (Davidson & Clark, 1985a) with around 150 originating from just 17kms stretch of coastline on the Wash (Davidson & Clark, 1985b). Redshank corpses were recovered at Teesmouth only during February (Davidson & Clark, 1985b). During late February 1986, 261 Redshank corpses were recovered from the Wash, but none from Teesmouth (Clark & Davidson, 1986).

The most recent large scale mortality of Redshank (and other shorebird species) occurred in February 1991. A total of 1553 Redshank corpses were recovered from the Wash (Clark *et al.*, 1993). The first reports of corpses on the Wash were received on 16 February, but the state of corpses suggested that the birds started dying around 10 February (Clark *et al.*, 1993). At Teesmouth 70 Redshank corpses were recovered from 12-17 February 1991 (pers. comm. R. M. Ward).

3.2 Methods

3.2.1 Measurement of Standard Metabolism: Open-flow Respirometry

A total of 15 *robusta* and 15 *britannica* were caught at Teesmouth and held in captivity under the conditions described in section 2.2.3 for periods of 1-18 months between October 1992 and March 1995. Birds were taken into captivity only if racial identity had been assigned (using the discriminant function of Summers *et al.* (1988)) with a probability of 0.9-1.0 so as to minimise the chance of mis-identification. In total 99 and 102 measurements of SMR were performed on *britannica* and *robusta* respectively at ambient temperatures T_a of -5, -3, 0, 2, 5, 7, 10, 12, 15, 17, 20, 22 and 25°C. Individuals were kept for a minimum of two weeks before any SMR measurements were taken to allow for adjustment to their new surroundings. Body mass generally fell during the first few days of captivity. The acclimation period allowed body mass to stabilise and body composition to adjust to the new feeding regime (see sections 2.3.6 & 2.4.3). Measurements were made only between October and early April, on individuals which were not in moult or undergoing substantial premigratory fattening. I have assumed that during this so called 'winter' period BMR scales with body mass within an individual by a constant factor. This is not an unreasonable assumption since during winter, the mass of lean metabolically active tissue remained constant within captive individual Redshank, with changes in body mass attributable only to changes in the mass of fat (see chapter 2). Furthermore, Scott *et al.* (1996) demonstrated that changes in BMR are best explained by changes in total body mass in captive individual Redshank whose body mass changes resulted only from changes in mass of fat. Measurements were performed on pairs of individuals consisting of one bird from each race ensuring that the results for either of the races were not seasonally biased.

SMR determinations were made in the open-flow respirometer described by Scott *et al.* (1996). Birds were placed in a sealed darkened metabolic chamber measuring 24.5cm (height) x 21cm (diameter) which was kept at a constant temperature in a controlled temperature cabinet (LMS, Sevenoaks, Kent). Metabolic heat production was measured by determinations of oxygen consumption using a paramagnetic analyser (OA/272 Taylor Servomex Ltd., Crowborough, Sussex) and CO_2 production using an infrared analyser (Lira 300, Mine Safety Appliances Company, Pennsylvania, USA) in an open circuit system. Dry air at T_a (-5 to 25°C) was drawn through the chamber at a rate of 60 L/h. Gas analyses were performed on samples taken from the inlet and outlet gases via gas mass-flow controllers (3.6L/h for O_2 and 48L/h for CO_2). Both inlet and outlet gases were dried prior to measurement by passing over columns of dried coarse mesh silica gel. Calibration was performed before each days measurements using dry, oil-free gases of 100% N_2 and a certified mixture of 21% O_2, 0.03% CO_2 in N_2 (SIP Analytical Ltd.).

Measurements were made during the day, since Scott (1991) found the BMR of Redshank to be no higher when measured during the day than during the night; in contrast to the situation in passerines, which have a lower BMR at night (Kendeigh *et al.*, 1977). During measurements, a bird was removed from its cage at 09:00h GMT, weighed to the nearest gram using a Pesola spring-balance and then kept isolated and without food until being placed in the chamber at 11:00h. Measurements commenced at 14:00h after a period of at least 3 hours of acclimation to the metabolic chamber and 5 hours fasting. This period of fasting was long enough to ensure that the birds were in a post-absorptive state, since RQ was around 0.7 (see Blaxter 1989) and further fasting did not result in a lower metabolic rate (I. Scott unpubl. data). Measurements were taken over a period of 1h when the chamber was maintained at a constant T_a. Measurement were taken at 3 different temperatures in a single day, starting at the highest T_a and then decreasing by 5°C at a time. A pause of 45-60min was taken between each measurement run to allow the controlled temperature cabinet to stabilise at the new T_a (10-20min) and a further 30min to allow the bird to acclimate to the new T_a. During pauses, inlet gas concentrations were measured.

During each run measurements were taken every minute over 10min periods during which O_2 consumption and CO_2 production were stabilised at a basal level. The mean O_2 and CO_2 levels over these 10min periods were converted to standard temperature and pressure (at 273°K and 1 atm) and used to calculate RQ (CO_2 production/O_2 consumption) and SMR (O_2 consumption) expressed in W using an energy value of 20.1KJ per litre O_2 consumed, appropriate for an RQ of 0.7. Mass-specific SMR was calculated as $SMR/BM^{1.02}$ expressed in mW/g; where 1.02 is the mass coefficient for BMR i.e. the slope of the relationship between $\log_{10}$BMR and $\log_{10}$body mass in Redshank (Scott *et al.*, 1996).

Although the birds could not be observed whilst in the chamber, activity was assumed to be negligible once the birds had habituated to the chamber, based on observations of birds in darkened keeping boxes and since space was confined in the chamber. Posture whilst resting, which would affect their level of energy expenditure, was assumed to be the same in both races, based on observations of resting birds in the indoor aviaries.

The rate at which SMR increases with decreasing temperature below the zone of thermoneutrality has traditionally been described, following Scholander *et al.* (1950) as:

$$SMR = K_{es} * (T_b - T_a) \qquad \textbf{3.1}$$

where K_{es} (measured in this study in W/°C or mW/g/°C depending on whether SMR is mass-specific) is termed the "wet" thermal conductance. $_{TLC}$ has traditionally been estimated from plots of SMR against T_a by forcing a line through points obviously below T_{lc} to cross the T_a axis at T_a=T_b (e.g. Kersten & Piersma, 1987; Wiersma & Piersma, 1994). However, McArthur (1990) argued that empirical evidence and thermodynamic theory show that the regression line of SMR on T_a actually intersects the T_a axis (where SMR=0) at a value of T_a higher than T_b and equal to T_b+c where c is larger in animals with better insulation. A more suitable method for estimating T_{lc} which does not make the above assumption is the two-phase regression procedure (Nickerson *et al.*, 1989; Yeager & Ultsch, 1989). Unfortunately two-phase regression proved inappropriate for the SMR - T_a plots in this study since measurements had been taken at only a few temperatures in the thermoneutral zone. Kendeigh *et al.* (1977) predicted that the T_{lc} of a non-passerine of body mass 152g (the mean of those *robusta* on which SMR determinations were performed) was 19°C and for *britannica* (mean BM of 142g) was 19.2°C. Thus, when comparing the effects of temperature on SMR of the two races at T_a s below T_{lc} only measurements taken below a T_a of 10°C were used to ensure that the birds were in standard metabolism without the need to first estimate T_{lc} for each race. In describing the effect of T_a on SMR equation 3.1 was not used, to avoid assuming that $T_a = T_b$ when SMR = 0. K_{es} was taken as the slope of the linear regression of SMR on T_a:

$$SMR = b - (K_{es} * T_a) \qquad 3.2$$

3.2.2 Construction and Operation of Heated taxidermic mounts

The construction and calibration of the mounts were based on the procedures and equations given by Wiersma & Piersma (1994). A Redshank corpse was skinned and frozen. Subcutaneous fat was removed from the skin before freezing. The bill was kept attached to the skin and the legs discarded. The heat-loss from the surface of the legs of shorebirds in the cold is negligible due to a counter-current mechanism in the blood flow to the tissues in the legs. The frozen corpse was laid sideways on a bed of modelling clay so that half of the corpse was exposed. After coating exposed surfaces of clay and flesh with petroleum jelly, plaster of Paris was poured over the corpse. Once the plaster had set, the clay was removed and fresh plaster was poured onto the remaining side.

The plaster mould was used to make a cast of the skin-less Redshank in beeswax. Two lengths of 5mm diameter copper tubing, crimped closed at one end were heated and inserted in to the wax cast, running vertically and parallel, from the vent region of the posterior to just behind the nape of the neck. Both tubes opened at the posterior end and would house the heating element, thermocouple and thermistor. The wax cast was lightly sprayed with aerosol adhesive and then dusted in graphite powder which creates an electrically conductive surface during electrolysis. A 0.4mm coating of copper was electroplated onto the wax cast (which acted as the anode) using 1M copper sulphate ($Cu\ SO_4 . 5H_2O$) and 0.75M sulphuric acid solution in a 4L bath circulated by a magnetic stirrer, a copper cathode and a 7V DC (2 A) power supply. Once fully coated, a small hole was drilled in the middle of the ventral surface of the copper shell, through which the wax was drained by gently heating the cast and into which a wooden dowelling stand was inserted.

The inner surface of the defrosted skin was dusted with Borax powder before being put over the cast which was first covered in heat-conducting paste. The bill was glued into position and the opening in the skin sewn up with monofilament fishing line.

The mount was heated by a central core, in the form of a heating element inserted into the lower copper tube, rather than being incorporated in the copper shell as in other studies (Bakken, 1983; Wiersma & Piersma, 1994). This alternative heating system better simulates the way heat is dissipated in a live bird, from a central body core (represented by the heating element) through the blood vessels (copper shell) to the skin. The heating element was composed of two 1.3m lengths of Nickel-Tungsten heater wire (0.12mm diameter and 11.2 ohms/m) with a Calcium salt insulatory coating wound around a 1mm copper tube core and covered in a protective coating of epoxy resin (Araldite). The heater was powered by a 12V (14A) motorcycle battery. The temperature of the mount T_m was measured by a platinum resistor thermocouple (PT100) inserted in the upper copper tube inside the mount and maintained by a temperature controller (DTC 410 Tempatron Ltd., Reading, Berks.) at 41°C, the body temperature T_b of Redshank. Voltage input V and T_m (measured by a thermistor placed next to the PT100) were recorded every 20s by an 8-bit datalogger (SQ32, Grant Instruments, Cambridge). The temperature controller produced an on-off power input to the heater, so that voltage readings were either around 12V (allowances were made for variations in voltage output by the battery) or 0V. The mean of the voltage readings V_m was taken over a 1 hour period. V_m / V equals the proportion of time t_v that power was supplied to the heater. Therefore, the energy consumption of the mount H_m (W) is, according to Wiersma & Piersma (1994):

$$H_m = t_v * V^2 / R_m \quad 3.3$$

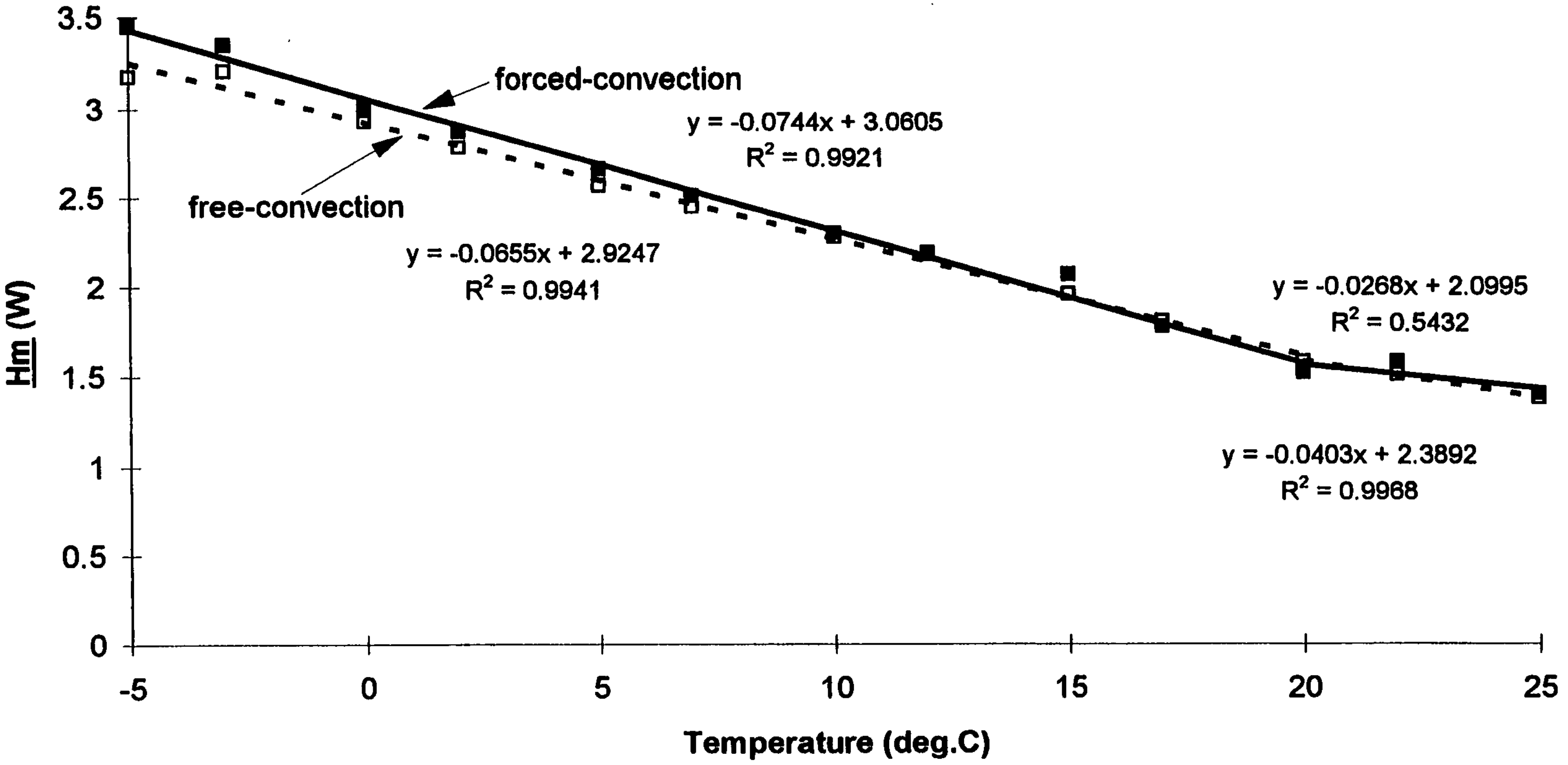
where R_m is the total resistance of the heater wire ($2*1.3m*11.2\Omega = 25\Omega$).

3.2.3 Calibration of heated taxidermic mounts

The methods and equations used to calibrate the heat loss from a taxidermic mount against that from a live Redshank and the theoretical basis for them are similar to those of Wiersma & Piersma (1994). However, my methods differ in two main respects. The first concerns the way in which the rate of heat loss of the mounts K_{esm} in a standard environment relates to a that of a live bird K_{es} . Bakken (1976) stated that the estimation of operative temperature T_{es} should be based on a value of K_{es} which represents heat loss due to radiation, conduction and forced (rather than free) convection. Hence, during SMR measurements forced convective heat loss has been stimulated by a fan situated in the metabolic chamber creating a standard wind (of 1m/s in the experiments of Wiersma & Piersma (1994)). They assumed forced convective heat loss to be zero when the fan was switched off. However, for this to be true, the air inside the chamber would need to be completely still, which is not the case in a metabolic chamber through which fresh air is constantly being pumped. Figure 3.1 illustrates that heat loss of a taxidermic mount was slightly but significantly greater when air was drawn through the chamber at a rate of 1.5L/min (the same air flow as used by Wiersma & Piersma, 1994) than when the chamber was completely sealed. Therefore, my value for K_{es} was derived in the same way that Wiersma & Piersma (1994) obtained their value of K_e (the rate of heat loss in a free-convection only environment). It is infact impossible to determine K_e in live birds using open-flow respirometry.

The second departure from Wiersma & Piersma's methodology was that I used mass-specific rates of heat loss for K_{es} and K_{esm} , $K_{es/g}$ and $K_{esm/g}$ respectively, measured as mW/°C/g rather than W/°C. Mass-specific values for K_{es} (i.e. $K_{es/g}$) allow for variation in body mass both within and between the individual Redshank

Figure 3.1: Relationship between energy consumption (Hm) and temperature of a heated mount of a British Redshank placed in a respirometry chamber with and without pumped air flow ('forced' and 'free' convection conditions respectively).



for which SMR was determined. Since it was the aim of this study to estimate M_{maint} over periods of several months when body mass changes were taking place, it was important to be able to allow for the effect of body mass changes on M_{maint}.

H_m was measured in a standard environment by placing the mount in the same metabolic chamber and exposed to the same temperature and acclimation regime as used for the live birds. In conditions of forced convection (flow through chamber of 1.0L/min) and below a T_a of 20°C, K_{esm} equalled 0.074 W/°C (Figure 3.1). In order to obtain a mass-specific temperature coefficient $K_{esm/g}$ in mW/°C /g for the mount in standard conditions, H_m at each temperature was divided by 157, the mass in g of the Redshank used to make the mount. The precise mass value used was incidental and only needed to produce a value of $K_{esm/g}$ of a similar magnitude to that of live Redshank, namely 0.47mW/C/g. This value did not increase over the period in which the mount was used, contrary to those of mounts used over a much longer period by Wiersma & Piersma (1994). The mass-specific heat loss of the mount $H_{m/g}$ was adjusted to that of a standard mount $H_{sm/g}$ with the same conductance as live Redshank of each race and core temperature of 41°C. Therefore $H_{sm/g}$ for a mount simulating the conductance of *robusta* was calculated as:

$$H_{sm/g} = 0.35*(41-(T_m-H_{m/g} / 0.47)) \quad \textbf{3.4}$$

where 0.35 was the mass-specific temperature coefficient for *robusta* in standard conditions. $H_{sm/g}$ for a mount simulating the conductance of *britannica* was calculated as:

$$H_{sm/g} = 0.30*(41-(T_m-H_{m/g} / 0.47)) \quad \textbf{3.5}$$

where 0.30 was the mass-specific temperature coefficient for *britannica* in standard conditions.

During February, March and April 1995 $H_{sm/g}$ was measured in a mount over periods of 1 hour when placed on a fixed site on Seal Sands mud flats where Redshank regularly feed. The mount was placed facing into the wind. Simultaneous hourly mean measurements of wind speed u (in m/s at a height of 10m) and air temperature T_a (°C) were obtained from a station at Graythorp (54°37'N 1°12'W) (supplied by Hartlepool Environmental Health Authority) 2Km from Seal Sands. Wiersma & Piersma (1994) incorporated direct hourly measurements of Global Solar Radiation (W/m^2) into their predictive model of M_{maint}. However, in Britain such measurements are taken by only a few stations and no such stations were situated near the sites being investigated in this study. A more commonly taken measurement is daily sunshine (measured in hrs). I estimated the daily total global solar radiation R_g (in W/m^2) using values of total monthly global radiation (measured in Kcal/cm^2/month) in a cloudless sky at a latitude of 55°N given in Lide (1990):

$$\text{hourly } R_g \text{ (Kcal/hr/m}^2\text{)} = (\text{total monthly } R_g * 10\,000) / (\text{no. days} * \text{total daylight hrs per month}) \quad \textbf{3.6}$$

$$\text{daily total } R_g \text{ (W/m}^2\text{)} = (1.163 * \text{hourly } R_g) * \text{daily sunshine hours} \quad \textbf{3.7}$$

where 1.163 is a conversion factor from Kcal/hr/m^2 to W/ m^2.

This estimate may be crude but gives an indication of the level of solar radiation experienced by the mount or live bird in the field. Radiative heat loss constitutes only 5% of the total heat lost through feathers (Walsberg, 1986); hence imprecise measurements of Rg would not lead to large errors when formulating a model predicting total heat loss in the field. Values of daily sunshine hours (supplied by the Meteorological Office, Bracknell) were taken from Tynemouth (55°1'N, 1°25'W) 49km from Seal Sands but the nearest station to obtain such information.

My model relating $H_{sm/g}$ (measured in mW/g) to measurements of u, T_a and R_g is of a similar form to that for H_{sm} (measured in W) given by Wiersma & Piersma (1994).

$$H_{sm/g} = (K_{es/g} + (K_u * u^y)) * (T_m - T_a) - (K_r * R_g) \qquad 3.8$$

The coefficients y, K_u and K_r were determined using non-linear iterative regression in SPSS.

In order to relate the heat loss of a standard mount $H_{sm/g}$ to the mass-specific maintenance metabolism $M_{maint/g}$ of live birds it is necessary to calculate standard operative temperature T_{es}:

$$T_{es} = 41 - (H_{sm/g} / K_{es/g}) \qquad 3.9$$

T_{es} combines all factors affecting heatloss and is thus a measure of environmental temperature. $M_{maint/g}$ was determined by substituting T_{es} for T_a in equation 3.2.

3.2.4. Estimation of M_{maint} and analysis of meteorological data at Teesmouth and the Wash

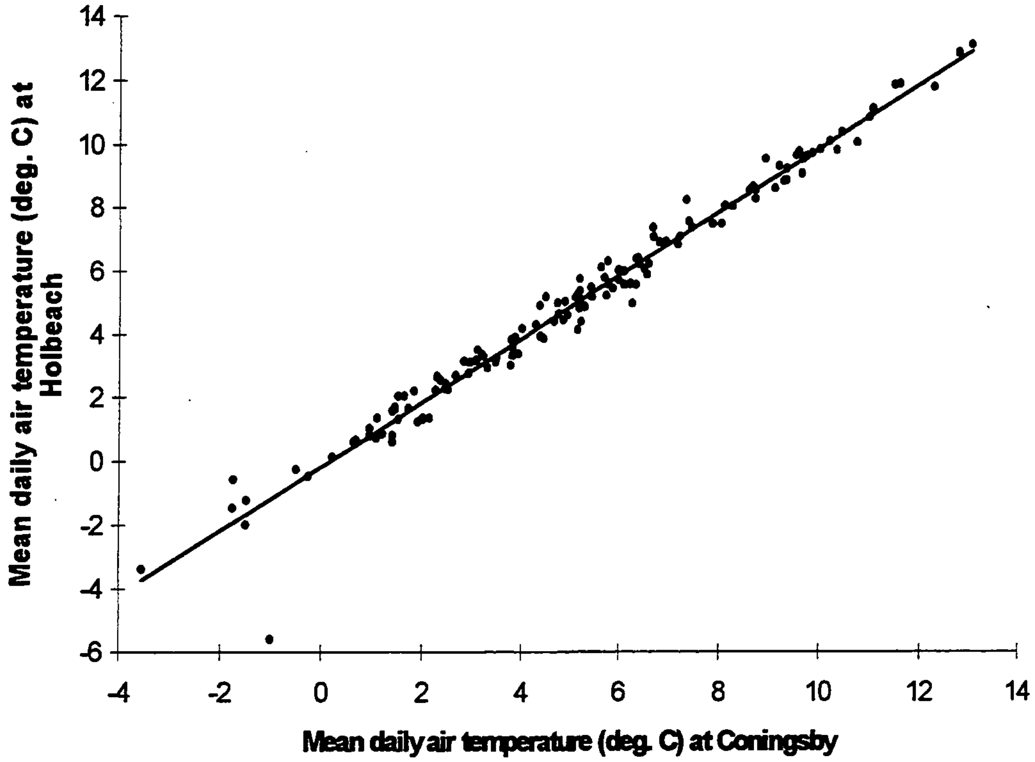
My aim was to obtain meteorological data which had been taken hourly so that daily total M_{maint} could be estimated, rather than using daily means (Kirby, 1995) as these may underestimate daily M_{maint}, since temperature and wind speed can vary greatly over 24 hours. The periods examined were from 1 November to 30 March for the winters 1978/79, 1981/82, 1984/85, 1985/86 and 1990/91 for both the Wash and Teesmouth; and additionally 1982/83 and 1983/84 at Teesmouth. All temperature and wind speed data were converted to units of °C and m/s respectively.

For the 1990/91 winter at Teesmouth, hourly mean wind speed (in m/s taken at 10m) and air temperature (dry bulb in °C) were obtained from Graythorp. Daily hours of sunshine were obtained from Tynemouth. $M_{maint/g}$ and T_{es} were calculated for each race during every hour using the models developed from Graythorp weather data described in section 3.2.3. (referred to hereafter as the 'Graythorp Model'). Unfortunately no further data were available from Graythorp for the other winters studied at Teesmouth. Therefore, wind speed (in knots at 10m) and air temperature (dry bulb in °C) records from the winters 1978/79 and 1981/82-1985/86 were obtained from the nearest available station at Newcastle Weather Centre (54°59'N 1°36'W) (supplied by the Meteorological Office, Bracknell) 50km from Seal Sands. A model was constructed to predict $M_{maint/g}$ and T_{es} at Teesmouth by incorporating wind speed and temperature measurements from Newcastle and sunshine hours from Tynemouth, and simultaneous direct measurements of $M_{maint/g}$ and T_{es} using the heated mount on Seal Sands, following the derivations described in section 3.2.3. The predictive power of this 'Newcastle Model' was found to be sufficient to estimate $M_{maint/g}$ and T_{es} of both races of Redshank at Teesmouth during the winters 1978/79 and 1981/82-1985/86 (see section 3.3.2 below).

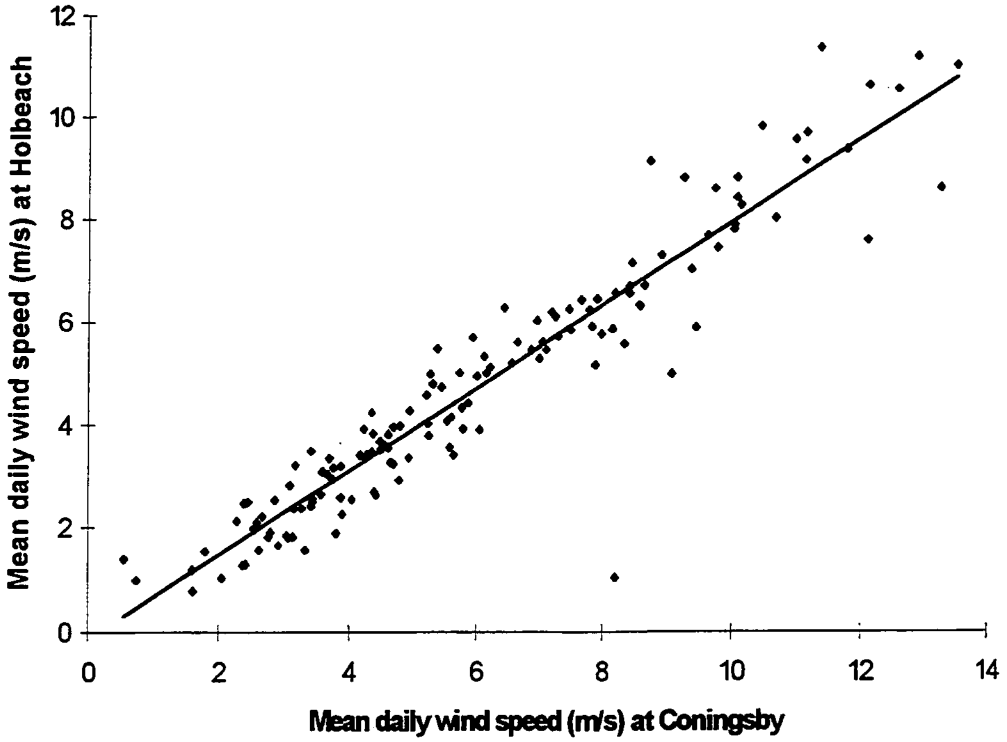
In order to predict $M_{maint/g}$ and T_{es} of both races of Redshank on the Wash during the winters 1978/79, 1981/82, 1984/85, 1985/86 and 1990/91, hourly mean wind speed (in knots at 10m) and hourly spot air temperature (°C dry bulb) were obtained from Coningsby (53°5'N 0°10'W) and daily sunshine hours from Terrington St. Clement (52°45'N 0°17'E) (all data supplied by the Met. Office, Bracknell). Coningsby is around 25km inland from the north-west coast of the Wash yet only 6m above sea-level and records similar values of wind speed and air temperature to those taken simultaneously at Holbeach (52°31'N 0°5'E) (Figure 3.2) situated just 2km from the west coast of the Wash (only incomplete data was available from Holbeach). Therefore Coningsby was an appropriate source of data indicative of conditions along the coast of the Wash. Additional justification for the use of met. data from Coningsby comes from the decision of the Nature Conservancy Council Working Group on setting up criteria for monitoring severe

Figure 3.2: Comparison of mean daily a) air temperatures and b) wind speeds recorded at Coningsby and Holbeach (Nov-Mar 1990/91). Regression lines denote exact equivalence.

a) Air temperature (R-squared = 0.98)



b) Wind speed (R-squared = 0.89)



weather to include Coningsby (along with Tynemouth) as one of 26 coastal stations used to define the severity of coastal weather when applying wildfowling ban legislation (Stroud, 1992).

The Graythorp model was applied to wind speed and air temperature data from Coningsby and sunshine hours from Terrington St. Clement to predict $M_{maint/g}$ and T_{es} of Redshank on the Wash; assuming that (i) weather conditions were similar at Coningsby and Holbeach; and (ii) that the Holbeach weather station is situated with similar relevance to the mudflats of the Wash as Graythorp is to the mudflats of Seal Sands at Teesmouth.

Additional data on 24-hour rainfall (mm), minimum daily grass temperature (°C) and the daily (at 09:00) presence and depth (cm) of lying snow were obtained from Tynemouth and Coningsby (Supplied by the Met. Office, Bracknell).

Hourly predictions of $M_{maint/g}$ measured in mW/g for each race at each site were converted into KJ/h for a Redshank of body mass equal to the mean body mass of the relevant race and month at Teesmouth (given in chapter 2). Values of hourly M_{maint} on each day were summed to give daily maintenance metabolism $M_{maint/d}$.

Several studies have suggested that Redshank that die following severe weather do so as a result of starvation rather than an inability to mobilise reserves fast enough (Davidson & Clark, 1985b; Beecroft & Clark, 1986; Clark & Davidson, 1986). If Redshank were starving to death, then the duration as well as intensity of high energy demands would be an important factor in determining survival during severe weather. The period of 1 November to 30 March was divided into five day segments or pentads The cumulative $M_{maint/d}$ over the five days equalled the total maintenance metabolism per pentad $M_{maint/p}$. Five days is a suitable time scale to use since it is long enough to be defined as 'prolonged' (voluntary wildfowling bans are imposed after just 7 days of continuous freezing (Stroud, 1992)), but not too short to smooth over short periods of very high energy demand, such as that on the Dutch Wadden Sea in January 1976 which led to mortality in Oystercatchers after less than 5 days of severe weather (Swennen & Duiven, 1983).

A critical minimum level of M_{maint} equal to 2.5 times BMR was used to indicate periods of energy expenditure which could potentially lead to, at best, a reduction in fitness or, at worst, death. A threshold of 2.5 times BMR assumes a maximum sustainable energy expenditure of 4 times BMR (see section 3.1.1) and a net cost of activity of around 1.5 times BMR. Speakman (1984) found the net cost of foraging in Redshank to be 0.7-0.9 times BMR. If this foraging cost is added to the cost of flying to and from feeding areas or when avoiding predators (8-12xBMR), it is not unreasonable to expect an average daily net activity cost of 1.5BMR, as found in breeding Turnstones (Piersma & Morrison, 1994). A threshold M_{maint} value of 2.5 times BMR proved to be a realistic level since, a threshold of 2 times BMR would define most winters as severe, whereas if 3 times BMR was used, no winter would be defined as severe. This critical level of 2.5xBMR equates to a $M_{maint/g}$ of 15.8mW/g and 18.0mW/g; and a T_{es} of -16°C and -15°C for *britannica* and *robusta* respectively. The equivalent values of $M_{maint/d}$ and $M_{maint/p}$ in KJ, taking into account monthly changes in BM of both races, are given in Table 3.1.

3.3 Results and Discussion

3.3.1 BMR and SMR of *robusta* and *britannica*

In order to remove any bias in the mean value of BMR (measured at 20, 22 and 25°C) of each race arising from some individuals being measured more times than others, the mean BMR for each race was taken as the mean of the average BMR of individuals. Mean BMR was 1.19W (SE=0.057) in *robusta* (n=14) with a mean mass of 151g (SE=5.3) and 1.01W (SE=0.073) in *britannica* (n=14) with a mean mass of 144g (SE=4.0). Due to large variances neither body mass (s^2=392 for *robusta* and s^2=228 for *britannica*) or BMR (s^2=0.046 for *robusta* and s^2=0.076 for *britannica*) were significantly greater in *robusta*. However, the mean mass-specific BMR for *robusta* of 7.2mW/g (SE=0.031) was significantly greater (T-test t_{26}=2.26 $P<0.05$) than the 6.3mW/g (±0.038) for *britannica*.

Table 3.1: Critical values for total Maintenance Metabolism per day ($M_{maint/d}$) and per 5-day pentad ($M_{maint/p}$) assuming an upper threshold of 2.5 times BMR and according to changes in mean monthly body mass.

Month (Pentad nos.)	**$M_{maint/d}$ (KJ) *britannica***	**$M_{maint/d}$ (KJ) *robusta***	**$M_{maint/p}$ (KJ) *britannica***	**$M_{maint/p}$ (KJ) *robusta***
NOV (1-6)	207	256	1034	1281
DEC (7-12)	210	253	1048	1266
JAN (13-19)	201	241	1007	1204
FEB (20-24)	196	242	980	1211
MAR (25-30)	192	231	960	1157

Figure 3.3 and 3.4 show for both races, the changes in mean SMR (W) and mean mass-specific SMR (mW/g) respectively with T_a. *T. t. robusta* appear to have both higher SMR and mass-specific SMR than *britannica* at all values of T_a. In order to determine whether this was solely a result of a higher BMR in *robusta* or was also due to a greater thermal conductivity; K_{es}, $K_{es/g}$ and intercepts of SMR/T_a and mass-specific SMR / T_a curves were calculated for values of T_a between 10°C and -5°C for each individual (Figures 3.5 & 3.6) to remove any bias resulting from SMR determinations being performed over a greater range of temperatures in some individuals than others. The mean of individual SMR's (Figures 3.5) and mass-specific SMR's (Figures 3.6) were significantly higher for *robusta* at all values of T_a between -5°C and 10°C, since the mean intercept of individual regression lines was significantly greater (T-test t_{25}=2.709 P<0.02 for SMR; t_{25}=2.668 P<0.02 for mass-specific SMR). The means of individual K_{es} of each race were not significantly different. However, the mean of individual $K_{es/g}$ was significantly higher in *robusta* (T-test t_{25}=5.191 P<0.001).

3.3.2 Calibration of heated mount

Figure 3.1 shows that H_m below 20°C was significantly higher (Paired T-test t_9 =5.372 P<0.001) with pumped airflow through the metabolic chamber, under conditions similar to those in which SMR was determined in live birds than with no air-flow through the chamber. Table 3.2 shows the estimates for K_u, K_r and y obtained by iterative non-linear regression which would be inserted into equation 3.8 to estimate $H_{sm/g}$ in *robusta* and *britannica* from measurements of wind speed u, temperature T_a and solar radiation R_g. $M_{maint/g}$ (mW/g) predicted by the Graythorp and Newcastle models (incorporating measurements of u, T_a and R_g taken at Graythorp and Newcastle weather stations respectively) were not significantly different from simultaneous direct measurements of $M_{maint/g}$ taken from

Figure 3.3 : The relationship between temperature and mean standard metabolic rate (SMR) in two races of Redshank. Error bars indicate 2xSE, sample sizes are given in fig.3.4.

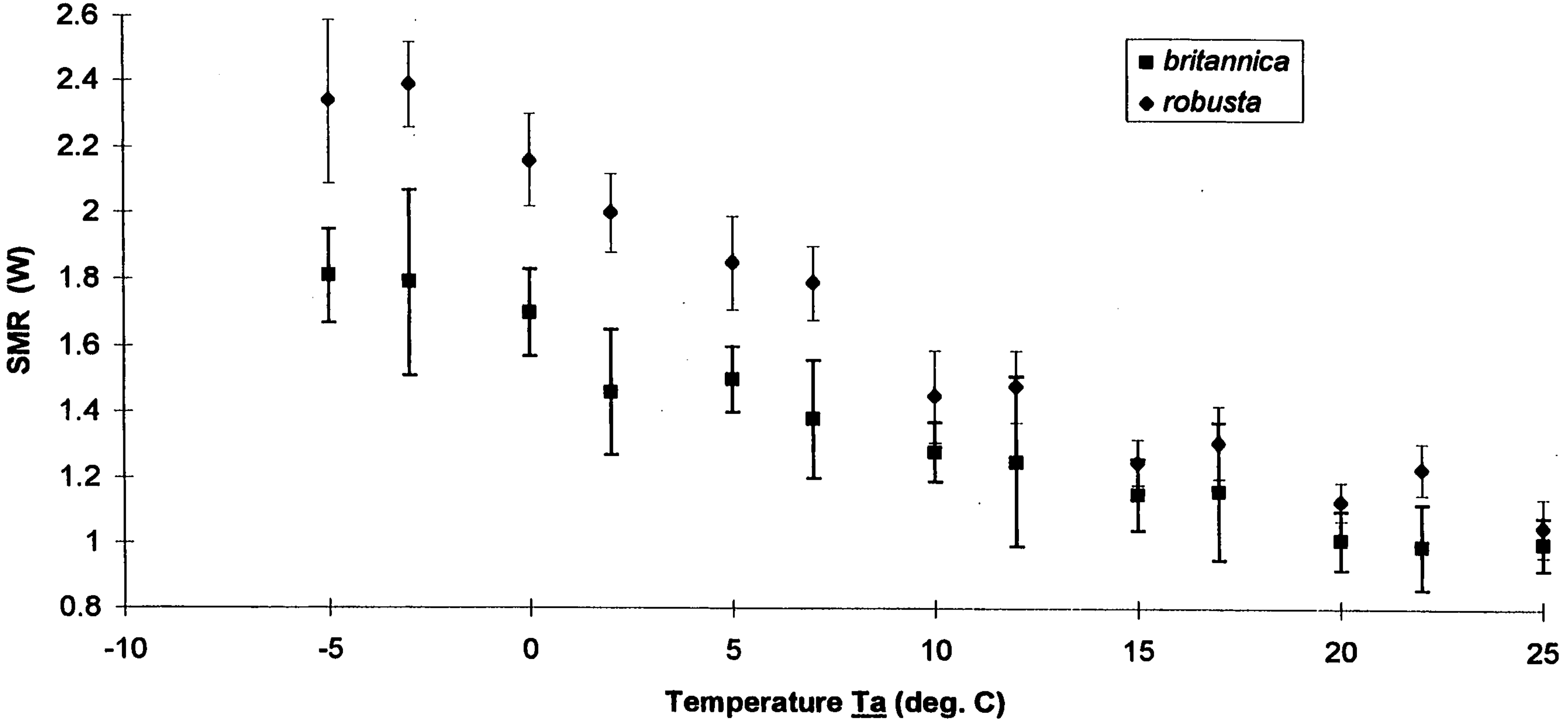


Figure 3.4: The relationship between temperature and mean mass-specific standard metabolic rate (SMR) in two races of Redshank. Error bars indicate 2xSE, numbers denote sample size.

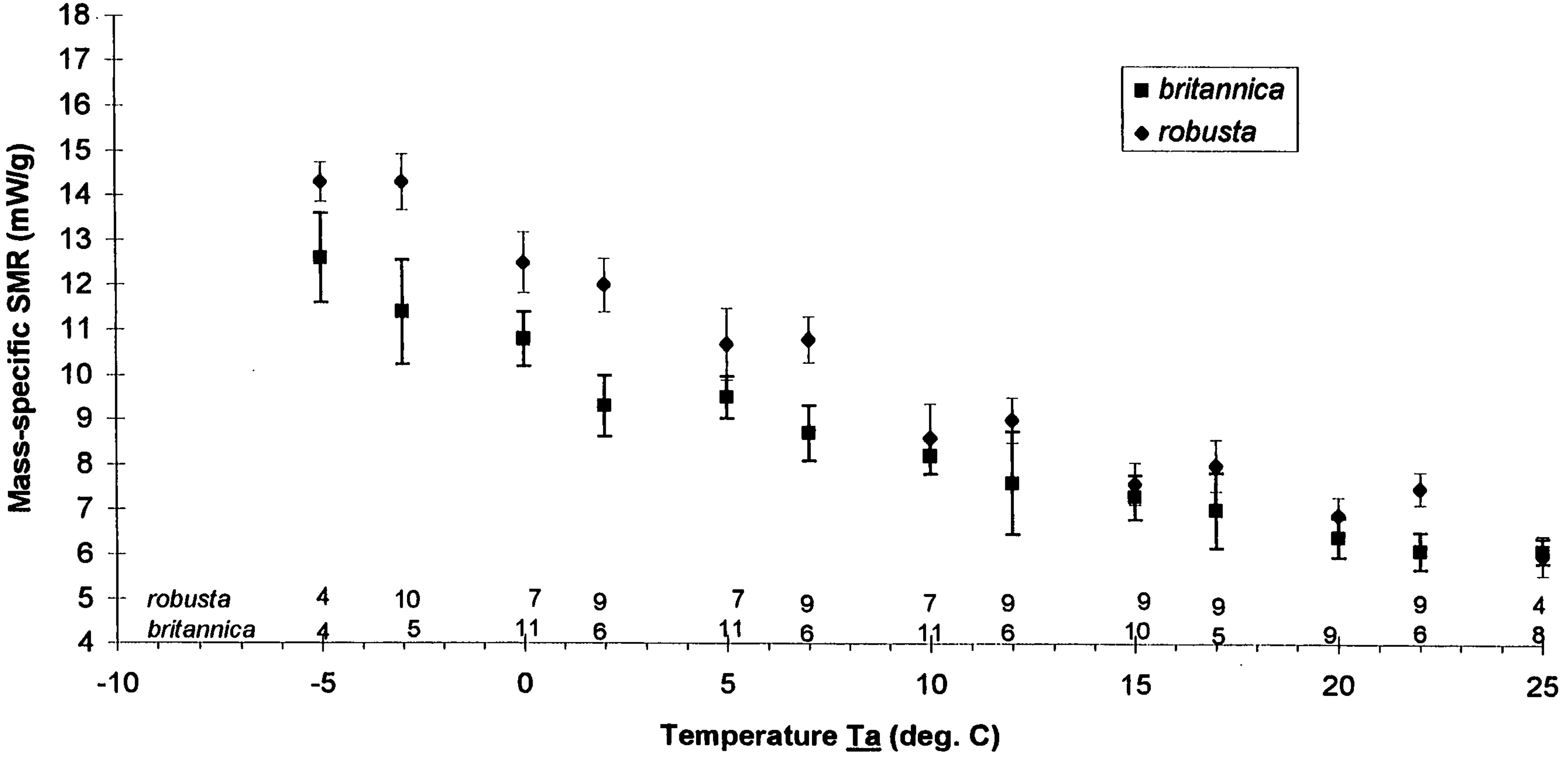
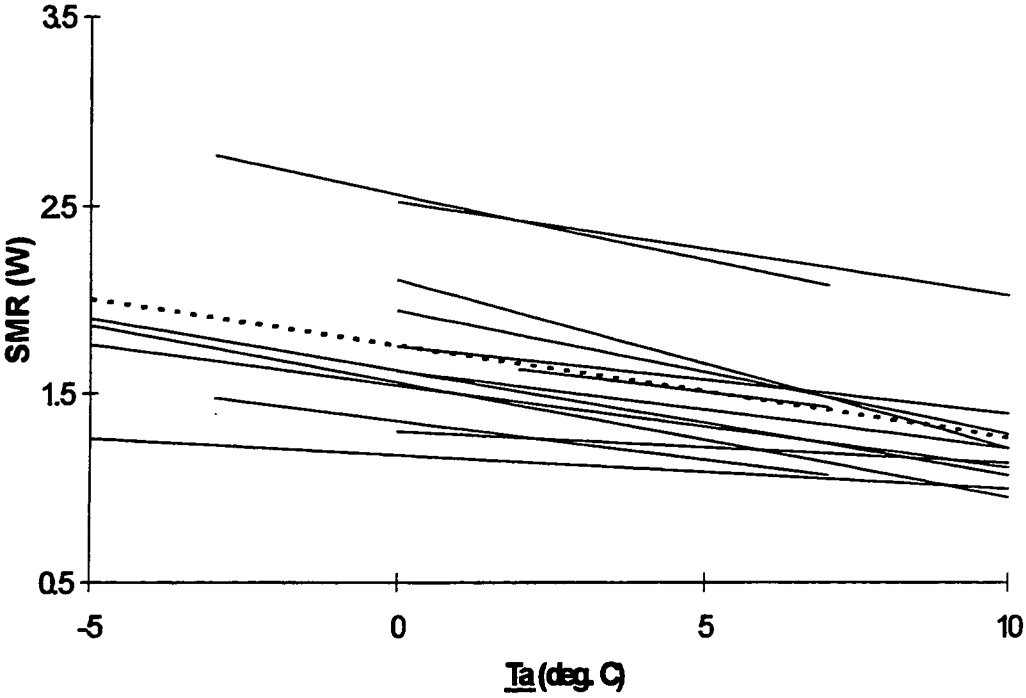


Figure 3.5: The relationship between standard metabolic rate (SMR) and Temperature (Ta) of individual a) *britannica* and b) *robusta*. Dashed lines denote the mean of individual trends.

a) *britannica*: SMR = 1.76 - 0.049Ta



b) *robusta*: SMR = 2.18 - 0.060Ta

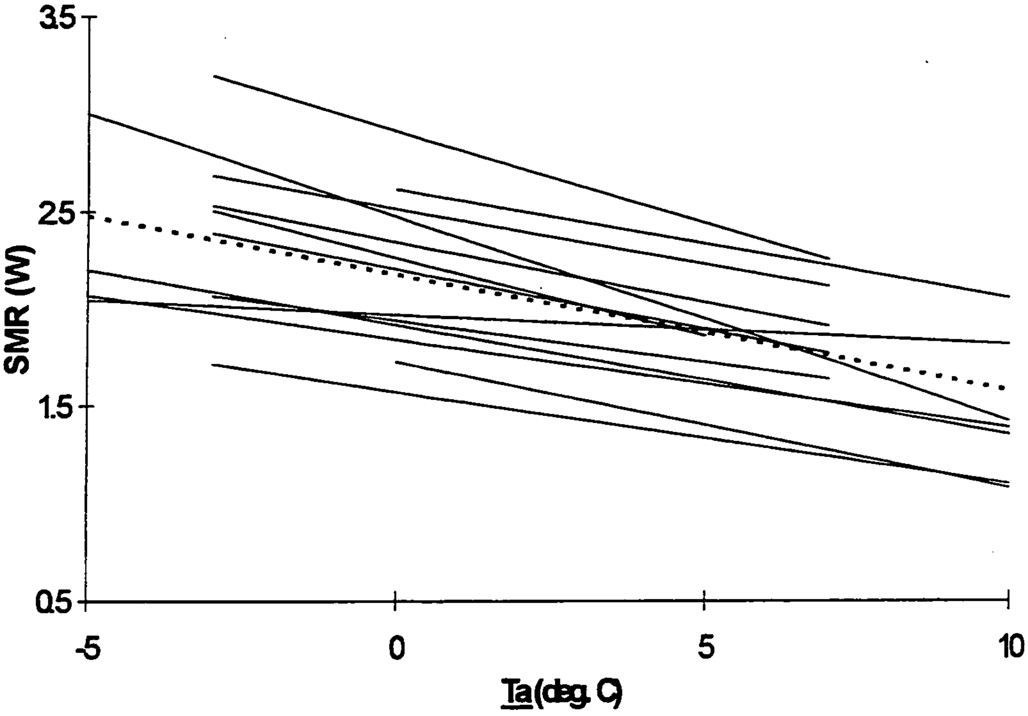
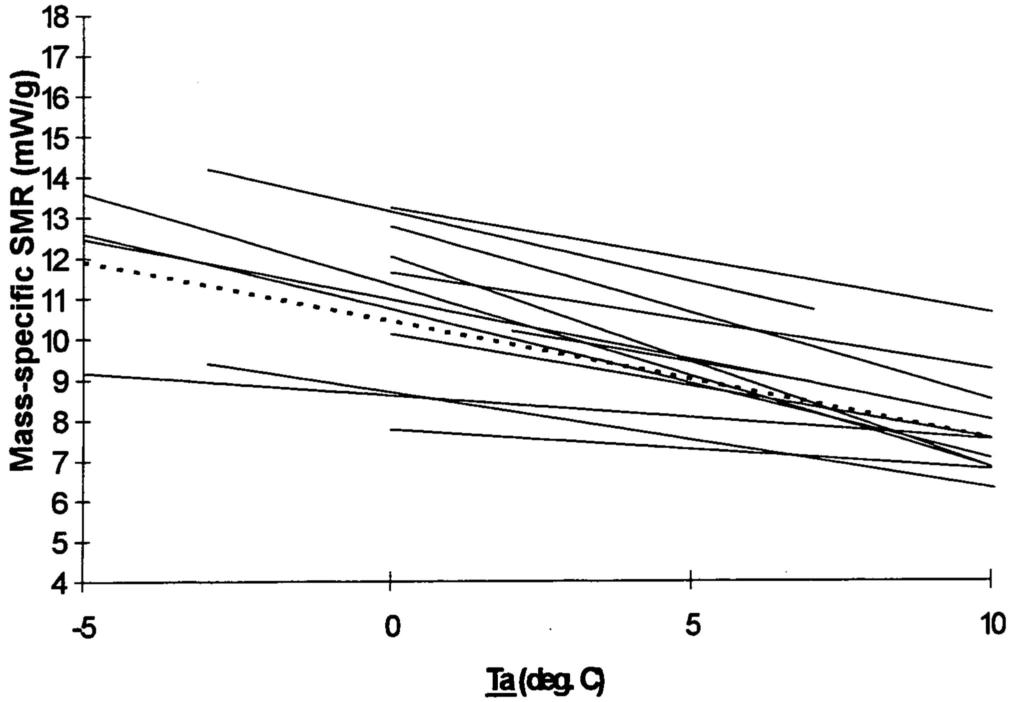


Figure 3.6: The relationship between mass-specific standard metabolic rate (SMR) and Temperature (Ta) of individual a) *britannica* and b) *robusta*. Dashed lines denote the mean of individual trends.

a) *britannica*: y = 10.98 - 0.30Ta



b) *robusta*: y = 12.76 - 0.35Ta

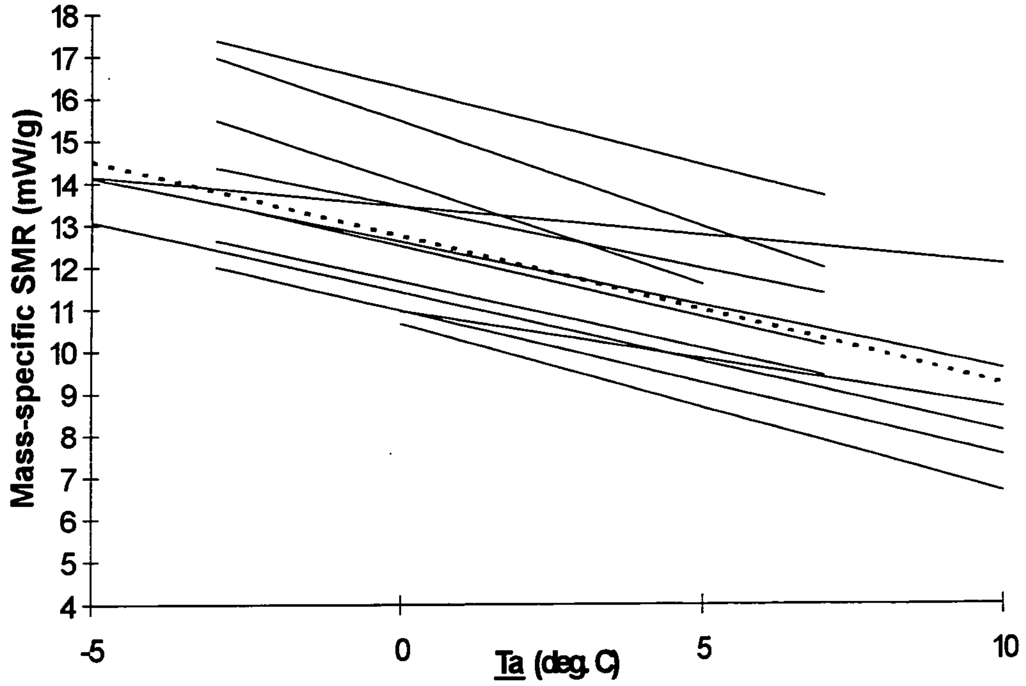


Table 3.2: Conductance parameters of *robusta* and *britannica* calculated from measurements of energy consumptio H_m of a heated taxidermic mount on Seal Sands mudflat, Teesmouth and of meteorological variables (temperature Ta, wind speed u, solar radiation Rg) taken from weather stations at Graythorpe and Newcastle using iterative nonlinear regression according to equation 3.8. Standard errors of estimates are in brackets. The regression was based on 51 hourly periods over which measurements were taken.

	$K_{es/g}$ (mW/°C/g)	K_u (mW/°C)	K_r (mW/°C)	y	r^2
Graythorpe	0.30	0.038	0.000040	0.78	0.65
britannica	(0.032)	(0.0089)	(0.000160)	(0.126)	
robusta	0.35	0.050	0.000052	0.78	0.65
	(0.098)	(0.0117)	(0.000211)	(0.126)	
Newcastle	0.30	0.074	-0.00016	0.43	0.52
britannica	(0.032)	(0.0136)	(0.00019)	(0.103)	
robusta	0.35	0.091	-0.00020	0.43	0.52
	(0.098)	(0.0168)	(0.00024)	(0.103)	

the heated mount at Seal Sands (paired T-test $t_{50} = 0.023$ $P>0.05$ for *britannica*, $t_{50} = 0.014$ $P>0.05$ for *robusta* predicted by the Graythorp model; paired $t_{50} = 0.0056$ $P>0.05$ for *britannica*, $t_{50} = 0.0048$ $P>0.05$ for *robusta* predicted by the Newcastle model). Hence, there was no significant difference between values of $M_{maint/g}$ predicted by the Graythorp and Newcastle models for both races (Figure 3.7: paired T-test t_{50}=. 0.989 $P>0.05$ for *britannica*; $t_{50} = 0.987$ $P>0.05$ for *robusta*).

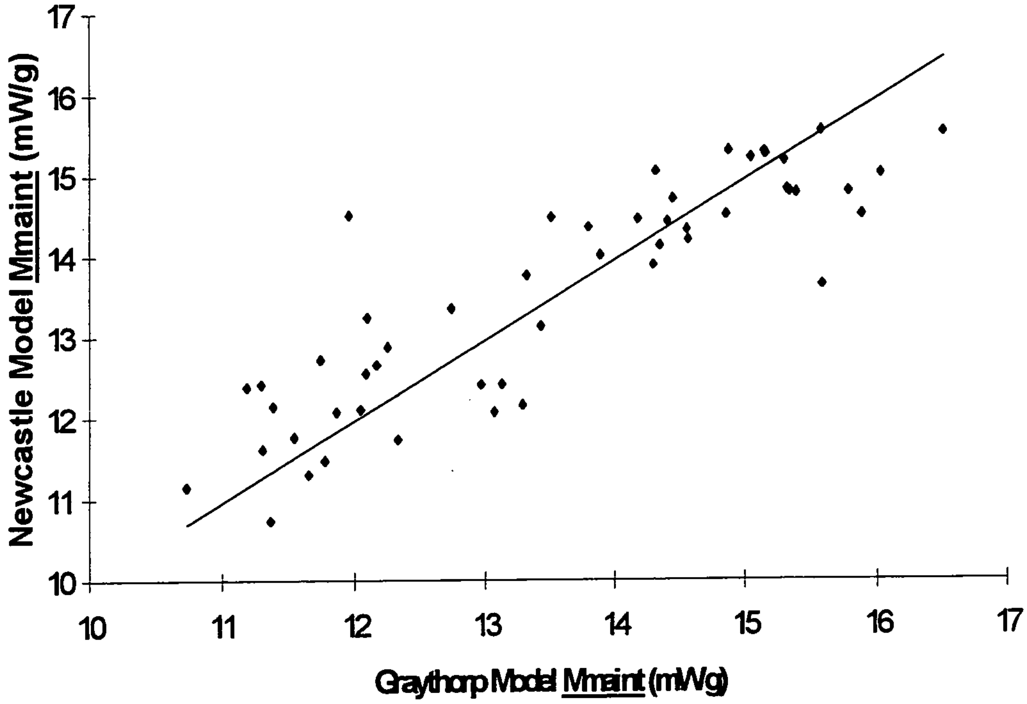
3.3.3 Maintenance metabolism during severe winter weather

Appendix III contains graphical representations of maintenance metabolism per pentad ($M_{maint/p}$) for both races, $T_{es,}$ air temperature and wind speed for each of the 30 pentads between between 1 November and 31 March within each of the winters examined (see section 3.2.4) at Teesmouth and the Wash. Periods of mortality are indicated as the pentads during which increases in mortality of Redshank were noted in the literature, usually by the recovery of large numbers of corpses (see section 3.1.4). This period was difficult to define at Teesmouth during the 1978/79 and 1981/82 winters since no large-scale recoveries of corpses were made, though mortality increased at some times during January 1979, February 1979, December 1981 and January 1982 (Davidson, 1982c).

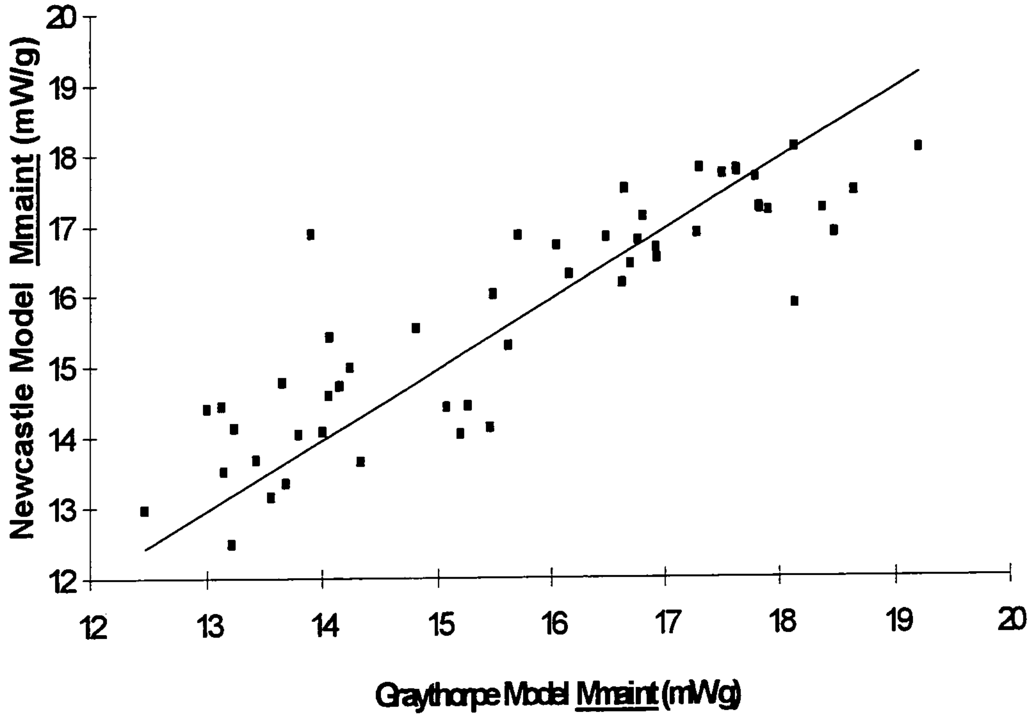
It is clear from the presentations in Appendix III that during those pentads in which mortality of Redshank occurred, $M_{maint/p}$ was higher than 2.5xBMR. A clear example of how an increase in $M_{maint/p}$ above 2.5 xBMR led to increased mortality was shown on the Wash in 1984/85 when $M_{maint/p}$ exceeded 2.5xBMR only during those pentads which were associated with increased mortality. The largest recovery of corpses of that winter occurred during February 1985 which held pentad 21 (9-13 February) in which $M_{maint/p}$ rose to 1556KJ in *robusta* and 1246KJ in *britannica*. During the same pentad mortality at Teesmouth coincided with $M_{maint/p}$ (of 1387KJ in *robusta* and 1112KJ in *britannica*) rising above 2.5xBMR

Figure 3.7: Maintenance metabolism (M_{maint}) of a) *britannica* and b) *robusta* predicted by models incorporating weather data from Newcastle Weather Centre and Graythorp weather station. Regression lines denote exact equivalence.

a) *britannica* (R-squared = 0.68)



b) *robusta* (R-squared = 0.68)



for only the second time that winter. It is also significant that increased mortality was recorded on the Wash but not at Teesmouth during pentads 13-17 (31 December - 23 January) when $M_{maint/p}$ either equalled or exceeded 2.5xBMR on the Wash but rose above 2.5xBMR only during pentad 17 at Teesmouth.

However, mortality amongst Redshank did not always increase significantly when M_{maint} rose above what was considered sustainable. Appendix III clearly shows that there were many occasions during the winters examined when $M_{maint/p}$ exceeded 2.5xBMR but no notable increase in mortality was recorded. For example, during the 1982/83 and 1983/84 winters at Teesmouth, when no increase in mortality was evident (Davidson & Clark, 1983b & 1984), $M_{maint/p}$ exceeded 2.5xBMR in *robusta* and *britannica* in 7 and 6 pentads respectively during both winters. Even within the same winter, the levels of M_{maint} which were associated with elevated mortality, were sometimes equalled or exceeded at other times when no notable rise in mortality occurred. This was most evident during 1985/86 on the Wash when the period of observed mortality which encompassed pentads 21-24 (9-28 February)(Davidson & Clark, 1986), was preceded by 9 successive pentads (24 December-8 February) during which $M_{maint/p}$ exceeded 2.5xBMR for both races and no mortality was evident.

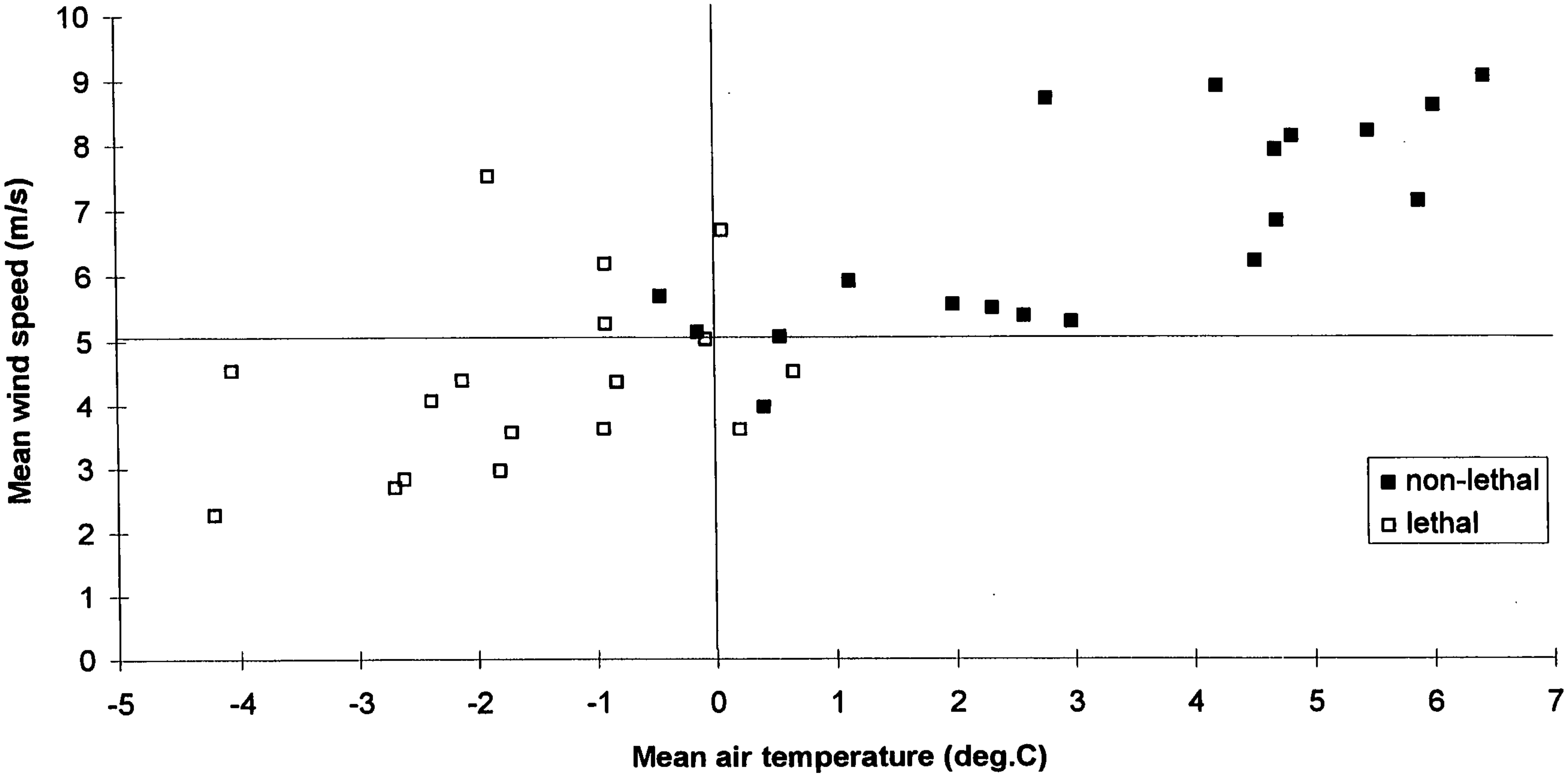
The weather associated with the non-lethal but apparently energy demanding period of pentads 12-20 1985/86 consisted of high winds (mean wind speed per pentad of 4-9m/s) but mean temperatures which remained above zero during all but two pentads (-0.5°C and -0.2°C in pentad 12 and 20 respectively). The period in which mortality occurred coincided with mean pentad temperatures dropping well below zero (mean temperatures of -2.6°C, 0.1°C, -2.7°C and -0.9°C during pentads 21-24 respectively).

This association between mortality in Redshank and prolonged sub-zero air temperatures (indicated by sub-zero pentad mean temperature) was consistent during all the winters examined. There was also a lack of association between mortality and prolonged periods of high windspeeds which could potentially create high values of M_{maint}. Figure 3.8 compares mean windspeeds and air temperatures of lethal and sub-lethal severe pentads (severe defined as when $M_{maint/p}$ exceeds 2.5xBMR and lethal pentads being those associated with mortality) on the Wash during the winters 1981/82, 84/85, 85/86 and 90/91. There is almost a clear separation in figure 3.9 between pentads which coincided with mortality and those which did not. The latter generally had mean temperatures above zero and mean windspeeds above 5m/s, whilst the 'lethal' pentads consisted of sub-zero mean temperatures and a wider range of low to high wind speeds.

It appears therefore, that the occurrence of severe weather mortality in Redshank was consistent with high levels of M_{maint} resulting from a lowering of T_{es} as a result of sub-zero air temperatures rather than solely from the large chilling effect of high winds. In actual fact, the potentially lethal chilling effect of high winds in producing very low values of T_{es} was not fully realised, suggesting that the Redshank were able to reduce their exposure to very high winds. The methods by which they could do this will be discussed later.

Since sub-zero air temperatures are well correlated with Redshank mortality, the intensity of freezing should be a good indicator and predictor of mortality. One measure of freezing intensity is the Hellman number, which is the sum of all temperatures below 0°C over a particular period. The Hellman number is often calculated from daily mean temperatures and applied to periods of several months to define and compare the severity of different winters (e.g. Ridgill & Fox, 1990). However, my study was concerned more with determining what level of air temperature would lead to mortality on a day-to-day basis. This was achieved by studying the period of mortality in February 1991, the only period for which there was accurate information on when the birds started dying. Figure 3.9 shows that, on the Wash, Redshank started dying 5 days after the daily mean air temperature

Figure 3.8: Mean windspeed and air temperature of severe pentads with ('lethal') and without ('non-lethal') association with mortality of Redshank on the Wash .



fell below 0°C and when the Hellman number (in this case, the cumulative sum of consecutive daily mean sub-zero temperatures) reached -10.6°C. At Teesmouth Redshank started dying 7 days after daily mean air temperature remained below 0°C, at a Hellman Number of -9.3°C.

If the numbers of corpses recovered were to be used as a measure of the severity of the effect of weather conditions on Redshank mortality, weather conditions during February 1991 would be considered the most severe of those winters included in this study. If this were true, the Hellman number would be predicted not to exceed around -10°C during any other pentad. However, Figure 3.10 shows clearly that all periods during which mortality was known to occur contain at least one pentad with a Hellman number of over -9°C, with one notable exception, Teesmouth 1984/85. During pentad 21 (8-12 February) which was associated with mortality at Teesmouth, the Hellman number was only -3.4°C. An explanation may be that this pentad had the highest mean wind speed of 5.9m/s of all the pentads with a non-zero Hellman number. The Hellman number could also explain observed differences in mortality between the Wash and Teesmouth, particularly during 1985/86.

What is clear from Figure 3.10 and from Appendix III is that the period in February 1991 was not the most severe in terms of energy demand or weather conditions. Yet February 1991 resulted in the greatest mortality in Redshank compared to the other winters in this study, according to reported carcass recoveries. For instance, in pentad 15 (9-13 January) in 1982, Teesmouth and the Wash had Hellman numbers of -23.5°C and -21°C respectively (Figure 3.10e), yet on the Wash high numbers of Redshank corpses were found, whereas only two were found at Teesmouth.

Likewise, during 1978/79 at both Teesmouth and the Wash levels of M_{maint} of both races reached levels expected to cause substantial mortality given the values of

Figure 3.9 : Daily mean air temperature and cumulative Hellman number on the days before and after large numbers of Redshank started to die in February 1991 at Teesmouth (12 Feb) and the Wash (10 Feb).

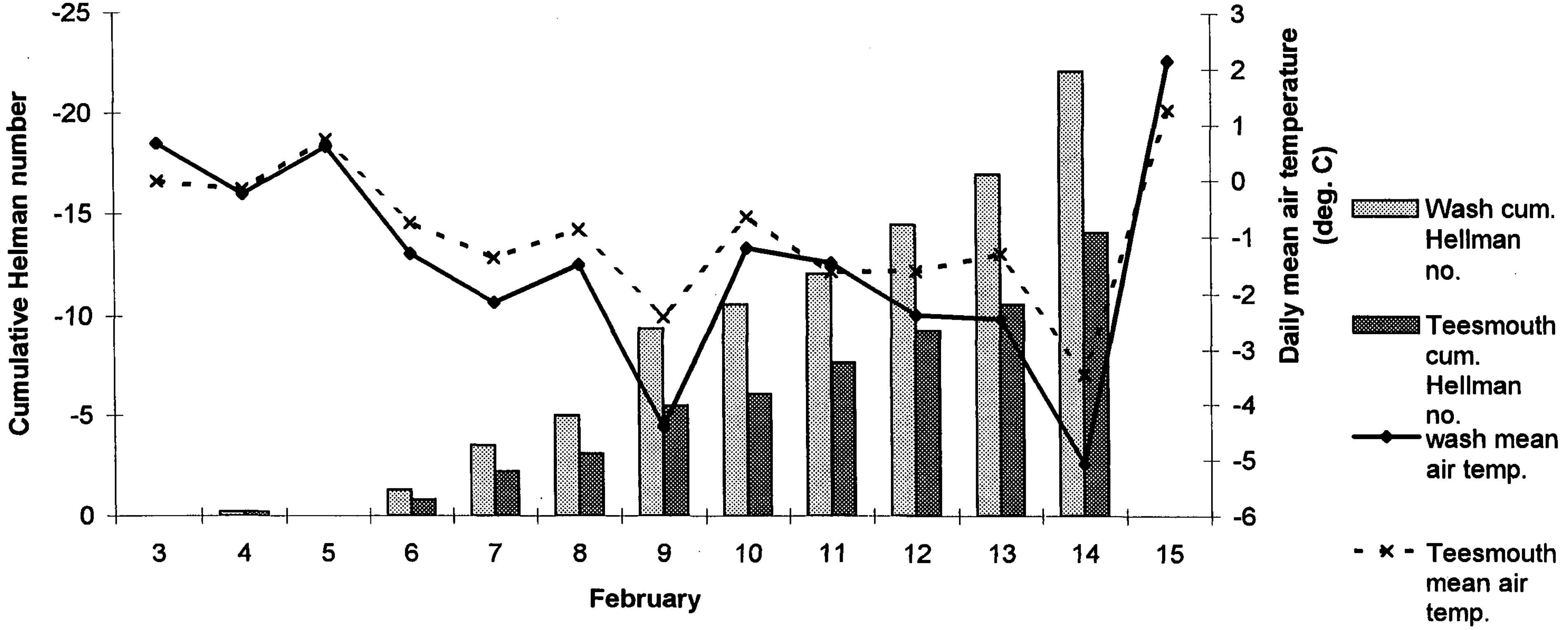
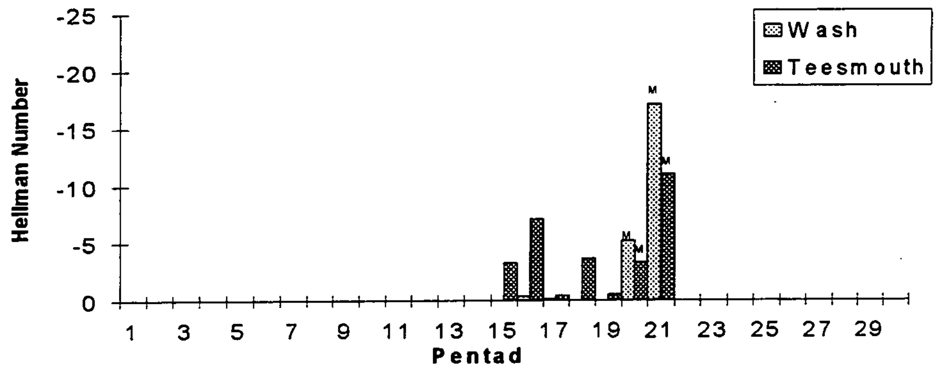
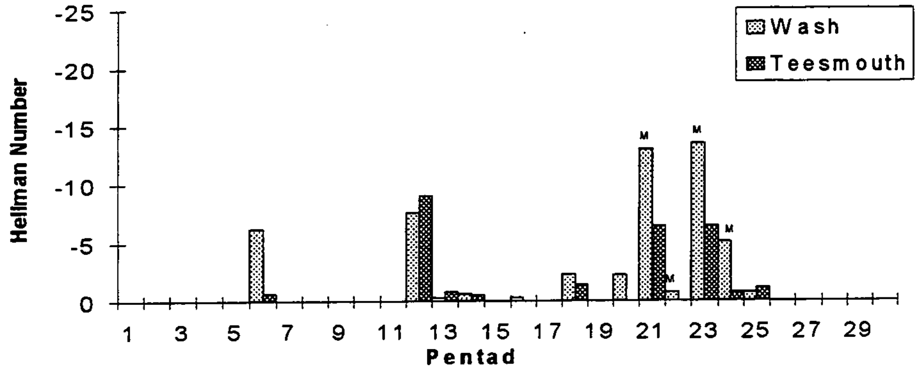


Figure 3.10: Hellman number of each pentad during the winters of a) 1990/91, b) 1985/86, c) 1984/85, d) 1982/83 & 1983/84 (Teesmouth only), e) 1981/82 and f) 1978/79 at Teesmouth and the Wash.

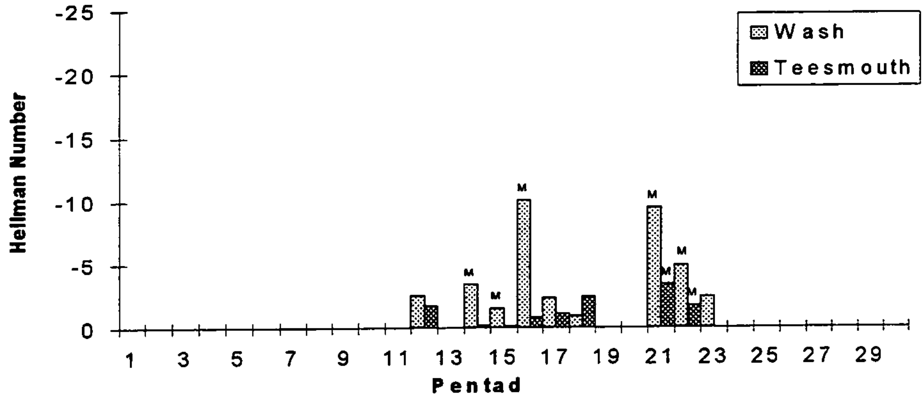
a) 1990/91



b) 1985/86

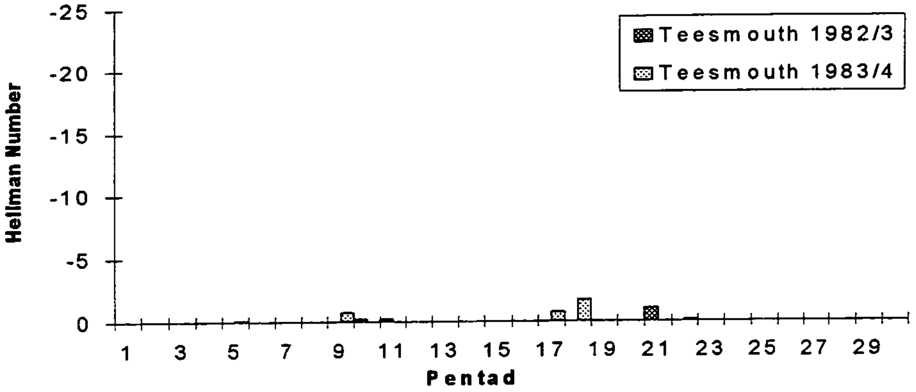


c) 1984/85

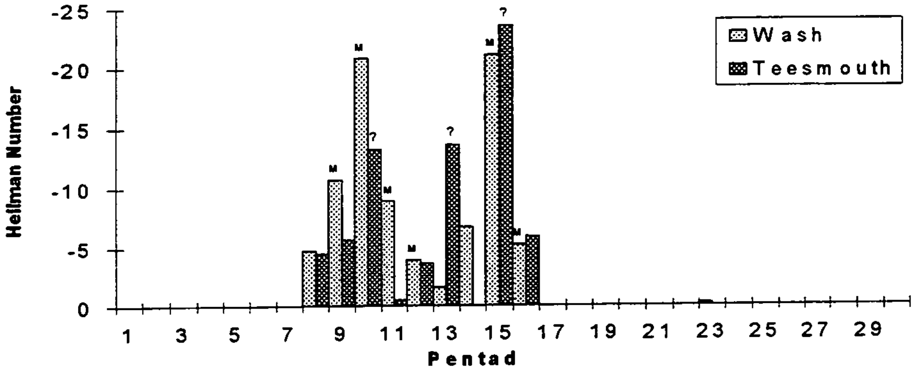


'M' indicates pentads which were associated with Redshank mortality. Pentad numbering started on 1st November and ended on 30th March.

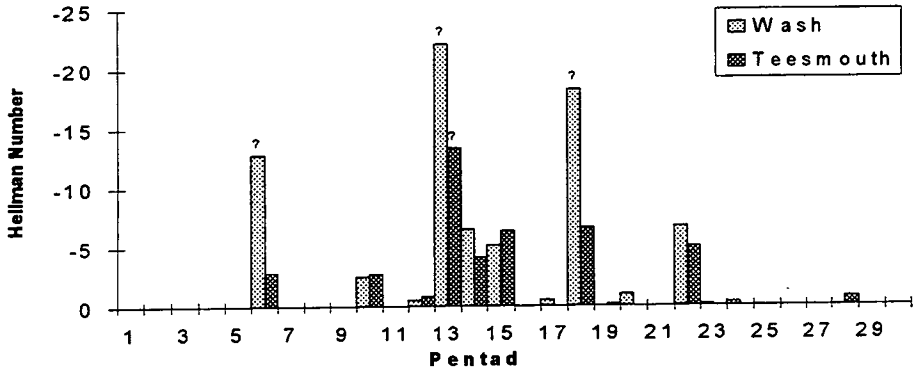
d) 1982/83 & 1983/84



e) 1981/82



f) 1978/79



'?' indicates those pentads with high Hellman which might have been expected to be associated with Redshank mortality, but were not.

M_{maint} associated with mortality in subsequent years (Appendix III). The high levels of M_{maint} during 1978/79 resulted in part from very high winds, but these were often accompanied by freezing temperatures, as shown by the high Hellman numbers in Figure 3.10f.

3.4 General Discussion

3.4.1 BMR and SMR

The significant difference between the mass-specific BMR of 6.3mW/g in *britannica* and 7.2mW/g in *robusta* has two possible explanations:

i) During their annual cycle the Icelandic Redshank *robusta* require the highest rates of metabolic output from their tissues during their migrations (1600km between Iceland and Britain), but are unable to alter the mass-specific output from their tissues and so must maintain a high mass-specific BMR throughout the year as an adaptation to their migrations (cf. 'Energetic Margin' hypothesis of Kersten & Piersma,1987). British Redshank move much shorter distances (at most 300km [Hale, 1973]) and would therefore not require as high an output from each gram of their muscles as their Icelandic conspecifics.

ii) Both races of Redshank have evolved a level of mass-specific BMR which is an adaptation to the rate of energy expended for thermoregulation in the respective climates on their different breeding grounds (cf. Weathers, 1979).

The 'energetic margin' hypothesis (Kersten & Piersma, 1987) assumes that birds are not capable of altering the metabolic output per gram from metabolically active tissues on a seasonal basis. There is conflicting evidence supporting and refuting the notion that birds cannot alter their mass-specific metabolic rate. In support, Knot over-wintering in west Africa had lower BMR's than their conspecifics in northern Europe, correlated with a lower total lean mass (taken as equivalent to the mass of metabolically active tissue) rather than a lower output per gram from the tissues (Piersma *et al.*, 1996). Conversely, Scott *et al.* (1996) found that the BMR of individual Redshank was correlated with the mass of fat being carried when lean mass remained constant, suggesting that the metabolic output of lean tissues was changing since the output from cellular fat is very low (Scott & Evans, 1992). Evans *et al.* (1992) found a higher density of mitochondria in the flight muscles of Sanderling and Dunlin sampled during long-distance migration than during winter, suggesting an increase in mass-specific metabolic output of muscles associated with migration. Marsh (1981) however, demonstrated that the aerobic capacity of muscles (as measured by concentration of Citrate Synthase, an enzyme of the Citric Acid Cycle) in the Gray Catbird (*Dumetella carolinensis*) remained constant during premigratory hypertrophy of flight muscles and Dreidzic *et al.* (1993) produced similar findings from a study of Semipalmated Sandpipers (*Calidris pusilla*) undergoing premigratory muscle hypertrophy and fattening. However, Dreidzic *et al.* also found an increase in the rate of fatty acid oxidation which would probably cause an increase in the mass-specific oxygen consumption of the muscles.

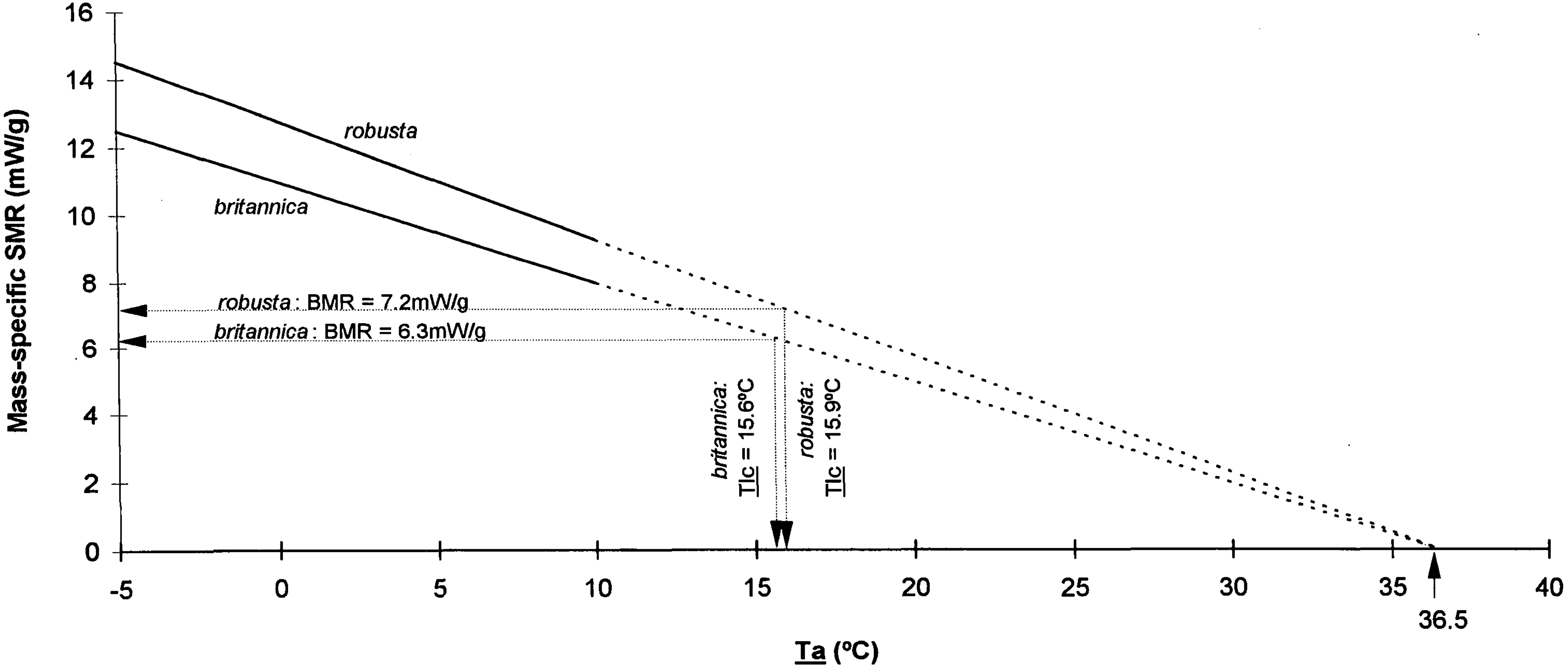
The alternative explanation for higher mass-specific BMR in *robusta*, is based on work by Weathers (1979) who found that the mass-specific basal metabolic rates of different species of bird were positively correlated with breeding latitude. Weathers explained this latitudinal trend in mass-specific BMR by adaptation to climate, with species at higher latitudes and in colder climates having a higher output per gram from their tissues in preparation for periods of high energy demand for thermoregulation. At lower latitudes in warm climates, high mass-specific rates of metabolic heat production may lead to excessive water loss and be detrimental to survival. Hudson & Kimzey (1966) demonstrated that within a species, the House Sparrow mass-specific BMR was higher in populations resident at higher latitudes in North America. However, *robusta* are migratory and therefore, an adaptation to the climate on the breeding grounds would be retained only if conditions on the wintering grounds were not counter-selective.

The essence of Weathers' theory is that for a given M_{maint} a bird with a higher BMR would be metabolising at a relatively (i.e. M_{maint} expressed as a multiple of BMR) lower rate than a bird of the same mass but with a lower BMR. Even though *robusta* had a higher mass-specific BMR than *britannica*, the former also had a higher thermal conductivity $K_{es/g}$ (in mW/°C/g) and hence a higher mass-specific M_{maint} than in *britannica*. Hence, for a given value of T_{es}, the ratio of M_{maint} to BMR is y : 1 in *britannica* but only (y+0.04) : 1 in *robusta*. Thus the energy expenditure for maintenance under the same thermal environment, relative to the basal output of tissues, is almost the same in both races. It is surprising that the apparent advantage of a higher BMR in *robusta* was cancelled out by a higher thermal conductivity.

Though the values for K_{es} of -0.049W/°C and -0.060W/°C of *britannica* and *robusta* respectively were not significantly different, they were 1.20 and 1.43 times greater than the values predicted by Kendeigh *et al.* (1977) (of -0.041 and-0.042W/°C respectively) for non-passerines of equivalent body masses. This compares with 1.14 times the predicted K_{es} in Oystercatcher, 1.30-1.42 times in Turnstone and Grey Plover (Kersten & Piersma, 1987) and 1.18 times in Knot (Wiersma & Piersma, 1994).

The difference in $K_{es/g}$ between the two races would initially suggest that the skin and feathers of *robusta* had poorer insulation or lower thermal resistance than those of *britannica*. However, by extrapolating the regression lines of mass-specific SMR on T_a (at $-5°C \leq T_a \leq 10°C$), of both races, back to values of SMR equal to i) their respective mass-specific BMRs and ii) zero, it can be seen from Figure 3.11 that the values of T_a at each intercept are similar for both races. The

Figure 3.11: The mean relationship between mass-specific standard metabolic rate (SMR) and temperature (Ta) of *britannica* and *robusta* between -5ºC and 10ºC (see Fig. 3.6), extrapolated to SMR=0mW/g.



lines intersect i) the lines for mass-specific BMR of each race at T_a = 15.6°C and 15.9°C (theoretical T_{lc}), and ii) the line SMR = 0 at T_a = 36.6 and 36.5 for *britannica* and *robusta* respectively. The implications of the similarity between races of these two intercept points is two-fold. Firstly, the thermal resistance and hence, insulation of the skin and plumage of both races must be similar (Kendeigh *et al.*, 1977; McArthur, 1991). Secondly, since mass-specific BMR was higher in *robusta,* the rate of heat loss represented by $K_{es/g}$, would also have to be higher. The thermodynamic equations of McArthur (1991) predict that if BMR is higher in one group, but that T_{lc} and the intercept of the T_a axis (and therefore thermal resistance) are all equal, then the total heat loss per unit of surface area below thermal neutrality would also be higher.

McArthur (1991) predicted that the SMR/T_a regression line should intercept the T_a axis (at SMR=0) at a value of T_a greater than T_b, in contrast to my study in which the opposite occurred, given that the body temperature of both races was around 41°C. McArthur's predictions were based on regression lines calculated over a range of T_a with T_{lc} as the upper limit, whereas in my study, the highest value of T_a in the regression was 10°C, somewhat lower than the T_{lc} of either race. It may be that the SMR of both races increased more rapidly with decreasing T_a at colder temperatures than at temperatures closer to T_{lc}, i.e. that the SMR/T_a regression would not be linear over the whole range of T_a, as a result of a reduction in the thermal resistance of insulating layers of tissue and feathers. Indeed, McArthur (1991) argued that even when the relationship between SMR and T_a is linear below T_{lc}, the thermal resistance may not necessarily remain constant. McArthur discusses evidence that suggests insulation may be reduced in increasingly cold temperatures since shivering can reduce thermal resistance of body tissue by up to 65%. Body movement also can reduce surface resistance of mammalian coats and disrupt the surface boundary layer.

The notion that the insulation by skin and feathers of the two races are indeed similar could be investigated empirically by measuring feather mass (Piersma *et al.*, 1995) or feather size (Summers et al, 1992); however both these characters are difficult to control for body size. A more objective but less simple method would be to measure heat flow through the skin and plumage using a heated plate/heat sink method as used by Walsberg (1988a).

It is therefore unclear whether the racial differences in BMR and SMR of Redshank found during the present study can be explained by either the 'energetic margin hypothesis' (Kersten & Piersma, 1987) or by breeding latitude (cf. Weathers, 1979). A comparison of BMR and SMR in different non-migratory populations of Redshank which breed at different latitudes would help to determine which of these hypotheses best explains racial differences in metabolic rate in Redshank.

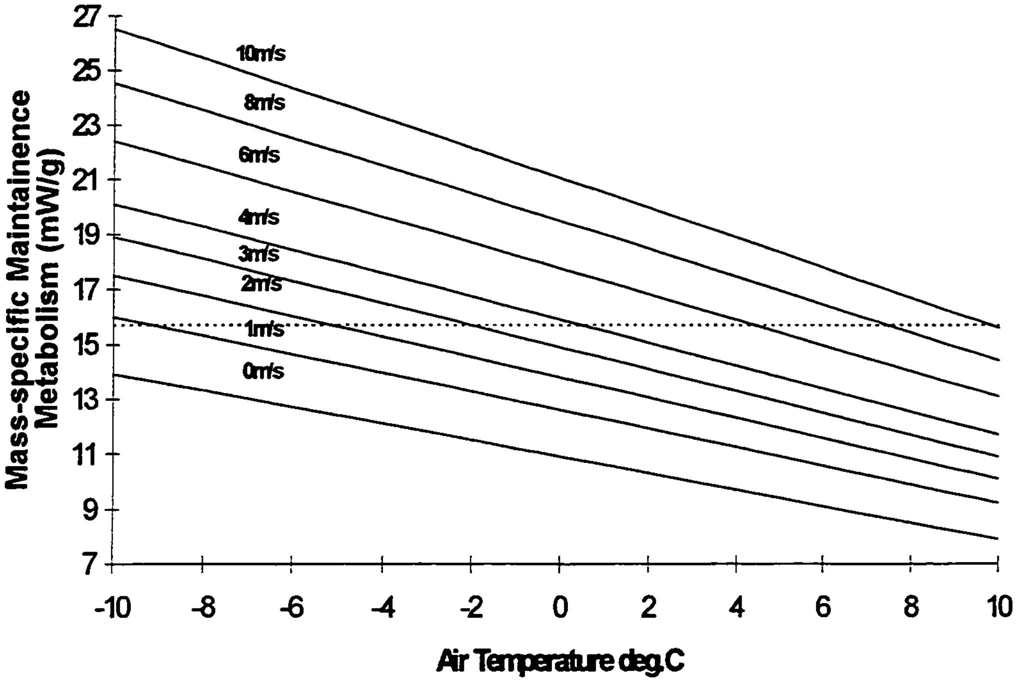
3.4.2 Energy expenditure and contributory factors during severe winter weather

It was clear from this study that large scale mortality in Redshank in Britain during winter occurred in part at least, as a result of maintenance metabolism costs exceeding a level of 2.5 times BMR. This threshold level was based on two assumptions: i) that DEE does not exceed 4xBMR without incurring a fitness cost (Drent & Daan, 1980); and ii) the net cost of activity is around 1.5xBMR (Piersma & Morrison, 1994; Speakman, 1984). This threshold level appears to have been appropriate, indicating that M_{maint} in Redshank rarely exceeds 2.5xBMR. This contrasts with Kirby's (1995) findings when using an M_{maint} threshold of 3.5xBMR (assuming a limit on DEE of 5xBMR) for defining the severity of the effects of weather on Knots. It may be that Redshank are not able to maintain, relatively, such a high level of energy expenditure as other shorebird species and are therefore more likely to die during periods of high energy demand.

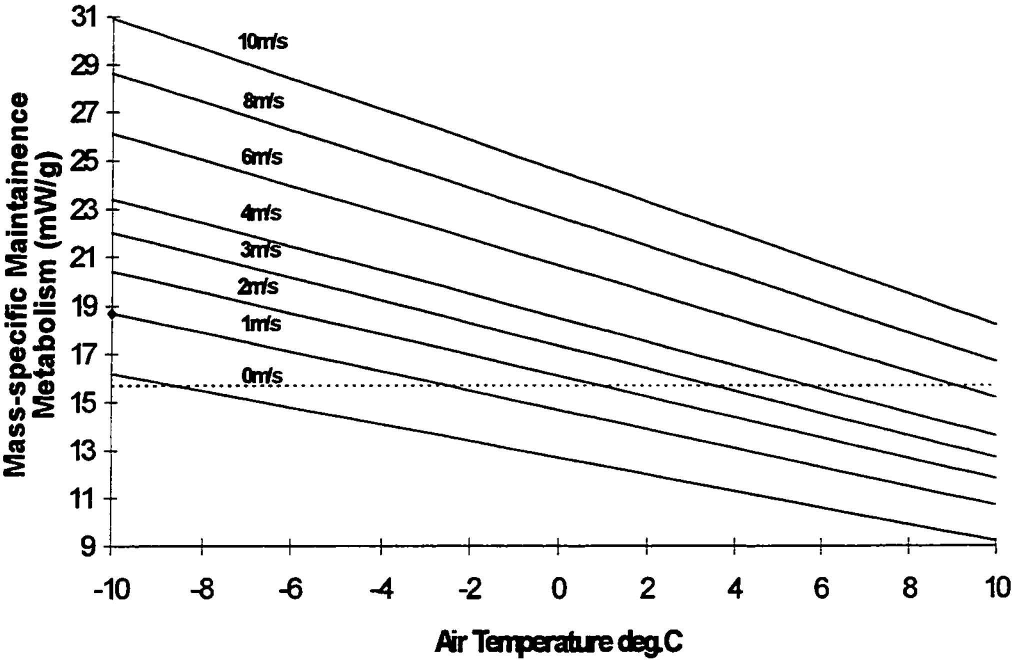
The imprecision of the estimated start time of severe weather mortality events made it difficult to ascertain what conditions on a daily basis caused increased mortality in Redshank. However by grouping days into pentads and incorporating a degree of longevity as well as intensity into measurements of M_{maint}, wind speed and temperature, it became clear that periods of prolonged sub zero temperatures were most influential in increasing Redshank mortality. A threshold Hellman number of -10°C per pentad or an average daily temperature of at least -2°C maintained for at least 5 days was consistent with mortality events. Indeed at such temperatures, the average wind speed would need to be only 1-2m/s to make M_{maint} of *robusta* exceed 2.5xBMR and 2-3m/s for *britannica* to do likewise (Figures 3.12 & 3.13). Mean daily windspeed rarely fell below 2m/s. However, the wind speed measured at 10m above ground was not what was actually experienced by the Redshank, in terms of its effect on T_{es} and M_{maint}. Redshank appear to be able to reduce the potentially high chilling effect of high winds by avoidance. Roosting in sheltered positions, in vegetation or in tight flocks can significantly reduce the effective wind speed (Whitlock, 1979; Wiersma & Piersma, 1994). Grey Plover are able to reduce the effect of wind whilst roosting, yet suffer high mortality only during severe weather events which included high winds as well as low temperatures such as in 1978/79 and 1985/86 (Davidson, 1982b; Clark & Davidson, 1986). Grey Plover are greatly affected by high winds whilst feeding, since the open mud-flats on which they feed provide little shelter, so that not only is wind-chill high, but food intake is significantly reduced (Dugan *et al.*, 1981). Redshank, however are more versatile in their feeding behaviour and are able to switch from feeding on exposed mud-flats to feeding in more sheltered areas such as creeks or amongst saltmarsh vegetation or on pastures inland. This ability to exploit less exposed feeding habitats is obviously crucial to Redshank and

Figure 3.12: The effect of air temperature and wind speed (m/s) on mass-specific maintenance metabolism of a) *britannica* and b) *robusta* on the Wash predicted from weather data at Coningsby using the Graythorp model.

a) ***britannica***



b) ***robusta***

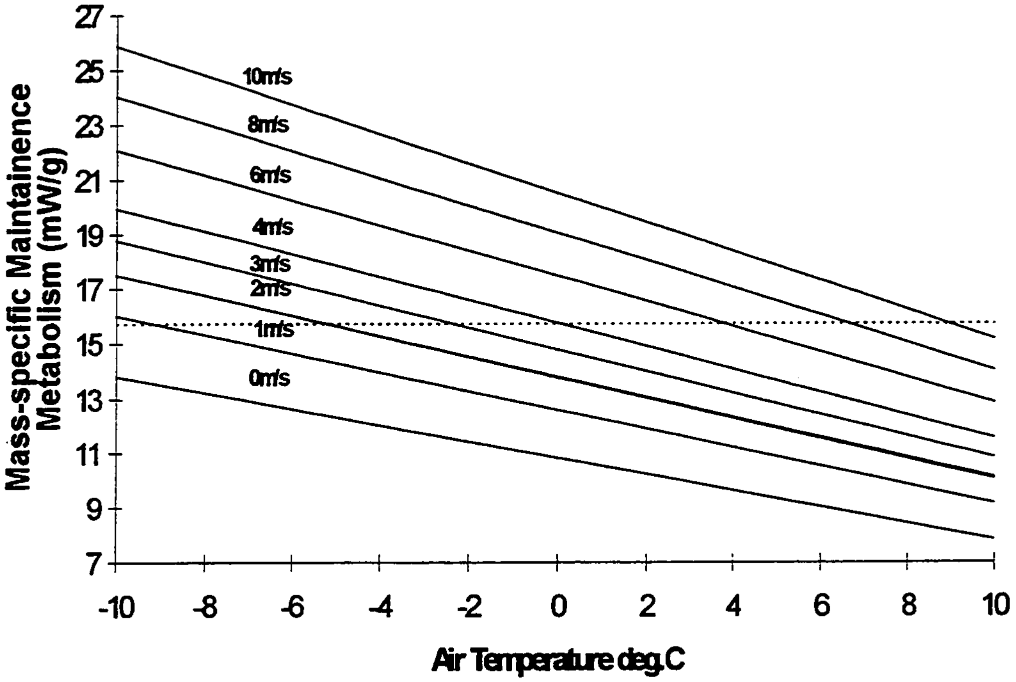


Dotted line indicates a maximum sustainable maintenance metabolism of 2.5xBMR.

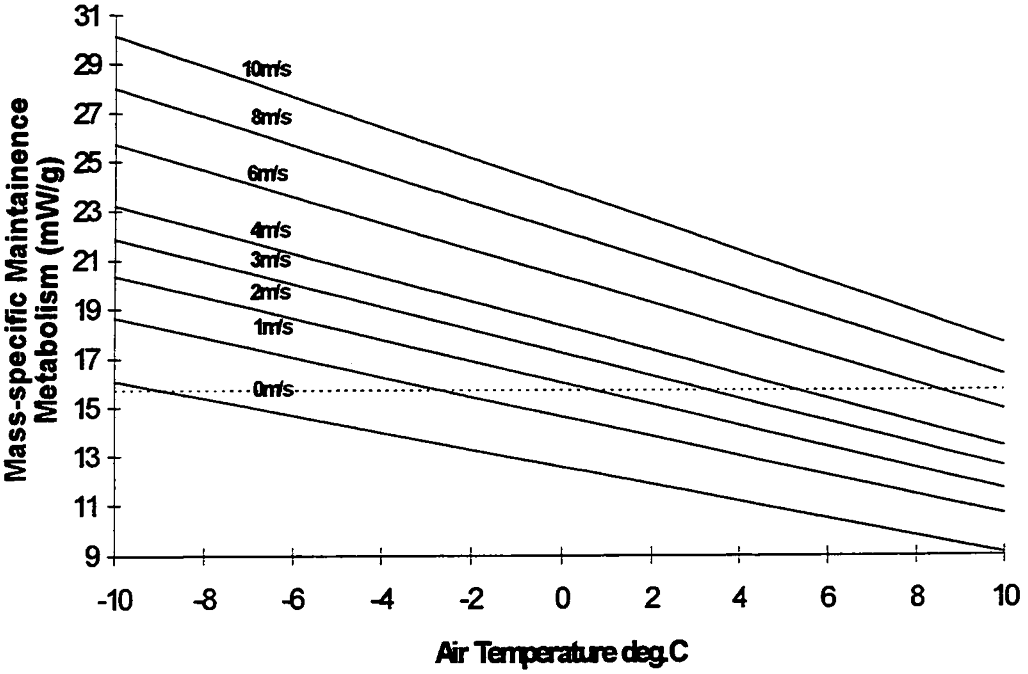
Daily global solar radiation is taken as 1000 W/m².

Figure 3.13: The effect of air temperature and wind speed (m/s) on mass-specific maintenance metabolism of a) *britannica* and b) *robusta* at Teesmouth predicted from weather data at Newcastle using the Newcastle model.

a) *britannica*



b) *robusta*



Dotted line indicates a maximum sustainable maintenance metabolism of 2.5xBMR.

Daily global solar radiation is taken as 1000 W/m².

other long-legged shorebirds in avoiding potentially lethal levels of M_{maint} during strong winds (Davidson, 1981).

The number of Redshank corpses recovered from the Wash in February 1991 were much greater than in previous 'severe' years during which conditions were in fact more demanding in terms of M_{maint} requirements. Clark *et al.* (1993) suggested that the timing of severe weather in relation to the tidal cycle could be crucial to the survival of shorebirds. They pointed out that during some years (including 1991), the period of severe weather which was associated with mortality coincided with high tides occurring during the middle of the day. Hence the majority of inter-tidal feeding areas were only exposed during darkness hours and may have lead to reduced food intake. However, Clark *et al.* (1993) did not show any consistent association between mortality events and the occurrence of high tides during daylight hours.

The scale of all mortality events which have occurred in shorebird populations has been assessed on the basis of the numbers of corpses which were recovered from the shoreline. A multitude of factors other than the number of birds actually dying, could affect how many corpses are found. For example, in February 1991, there may have been an increase in the awareness amongst observers of the effects of cold weather on shorebirds and hence, in the intensity and extent to which areas of shore were searched. The length of shoreline searched and the effort expended on the Wash during 1984/85 and 1985/86 were similar due to their inclusion in the WSG severe weather project. More corpses were recovered on the Wash in 1985/86 which could reflect the greater intensity of sub-zero temperatures in February 1986 (i.e larger Hellman numbers: Figure 3.10) compared to February 1985. The number of corpses recovered in 1981/82, though apparently more severe in terms of freezing temperatures (Figure 3.10) was less than during the subsequent 'severe' winters. This could be explained by the short length of coastline searched in 1981/82 and the sporadic nature of the search.

The low numbers of Redshank corpses recovered at Teesmouth during 1984/85-85/86 in comparison to the large number in 1991 could be explained by the lower severity of weather conditions and energy demand during these two winters. However, such explanations could not be used to account for the lack of corpses recovered during both 1978/79 and 1981/82. It may be the case that on the Wash, if a large proportion and hence a large number of the Wash population of Redshank die, the number of corpses found will depend almost entirely on search effort, whereas at Teesmouth other factors come into play. The majority of the main feeding grounds and roost sites of Redshank have restricted public access (due to requirements of industry) so that most corpses have to be found during planned searches and not by casual observers as on the Wash. Secondly, the timing of the searches at Teesmouth would seem to be crucial since there appears to be a high degree of scavenging and removal of corpses by both avian and mammalian predators/scavengers. For example all of the 70 Redshank corpses found in 1991 had been scavenged to some degree (pers. comm. R. M. Ward). An experiment using 25 feral pigeon carcasses revealed that all were removed from above the high spring tide mark at Teesmouth within 13 days of being placed there; 3 had already been scavenged within the first 2 hours (pers. obs.).

Whilst the estimation of mortality rates by ringing recoveries removes some of the problems associated with carcass searches, the latter is still a crucial exercise in estimating the start of a mortality event and for recovering carcasses for analyses of body composition, sex, age etc.

4.0 Foraging Behaviour

4.1 Introduction

This chapter discusses whether both races of Redshank are equally capable of meeting their energy requirements at any given time through feeding, given that i) *robusta* have larger daily energy requirements per gram of body mass for maintenance (Chapter 3); and ii) both races accumulate the same energy reserves in mid-winter in terms of fat (as a percentage of body mass) and protein (corrected for body size) (Chapter 2). The implication is that *robusta* would be expected to require a higher rate of intake of energy from food per gram of body mass. This may be achieved by: i) taking more prey per unit time, ii) taking larger and/or more energetically profitable prey items, iii) feeding for longer periods in each day.

4.1.1 Prey intake rate

The rate of food intake of Redshank has been shown to be dependant on the density of prey available (Goss-Custard, 1977c). Prey availability can in turn be affected by weather conditions and other environmental factors such as tidal movements (see Evans, 1976 for review). For example, at low air temperatures invertebrates tend to burrow deeper to more stable and warmer conditions and therefore may be less accessable to foraging waders. Foraging may be directly affected by weather as in the case of Grey Plovers whose foraging was hindered by buffeting during high winds (Dugan *et al.*, 1981). I investigated whether the effect of weather (i.e. air temperatures and wind speeds)on foraging was similar in both races.

4.1.2 Prey choice

Monitoring prey choice and prey size proved difficult since the majority of prey items taken were small and impossible to identify or quantify when taken. Based on other studies of Redshank diets (Goss-Custard & Jones, 1976; Goss-Custard *et al.*, 1977; Evans *et al.*, 1979) and of recent surveys of Seal Sands macro-invertebrate fauna (Evans*et al.*, 1996), small prey were assumed to be either small worms, the burrowing amphipod *Corophium volutator* or the gastropod mollusc *Hydrobia ulvae*. Overall food and energy intake could therefore not be measured in the present study by direct observation. However, large worms (e.g. *Nereis diversicolor*) were more conspicuous when taken and their frequency in the diet of *robusta* and *britannica* was compared. The intake of worms by Redshank at Teesmouth is low but increases with greater energy demands (Appendix IV; see also Goss-Custard, 1969). Large worms appear to be a valuable energy supplement when energy requirements are high. Worm intake may therefore be important in providing for the greater maintenance requirements of *robusta*.

Other methods of quantifying energy intake were deemed impractical, in that: i) analysis of gut contents would require the sacrificing of large numbers of birds in order to compare the seasonl food intake of the two races; ii) pellets could have been used to quantify diet (Goss-Custard & Jones, 1976) but the racial origin of the Redshank which produced them could not be determined.

4.1.3 Duration of feeding

Goss-Custard (1969) and Speakman (1984) suggested that Redshank in winter would have to feed both diurnally and nocturnally to achieve sufficient energy intake to satisfy their demands. In Appendix IV, I suggest that in Redshank there may be a trade-off between the amount of energy obtained from feeding in a given time and the amount of energy expended in doing so and consequently, the time spent feeding may get less as energy demands for maintenance increase. Therefore, *robusta* may not satisfy their greater maintenance costs simply by feeding for longer than *britannica*. Hence this study aims to compare the seasonal pattern of daily feeding duration of each race with that of the whole Teesmouth Redshank population (mixed race) described in Appendix IV.

4.2 Methods

4.2.1 Study Area

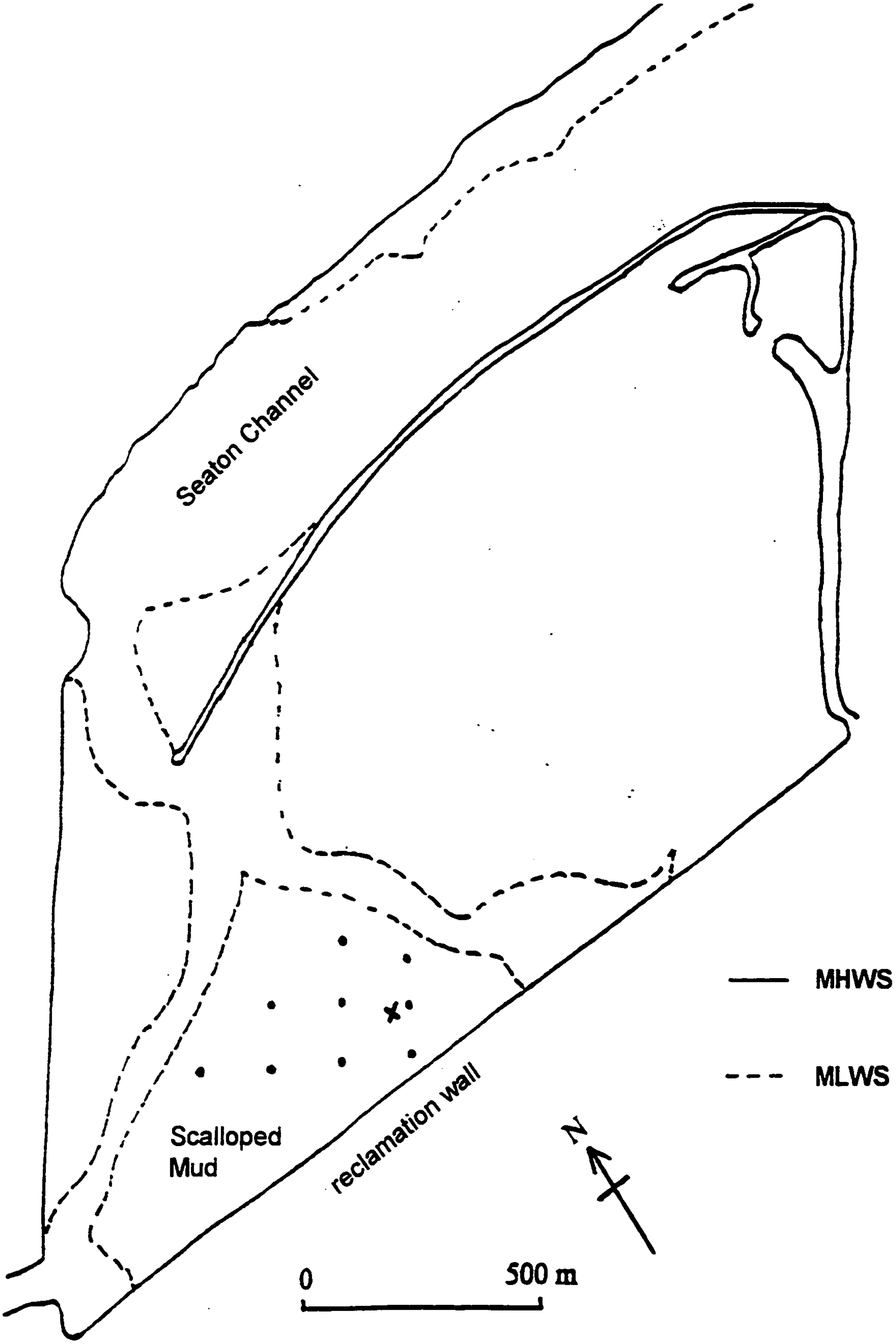
Observations of foraging behaviour were made at Seal Sands mudflats at Teesmouth in north-east England from October to March during the winters of 1993/94 and 1994/95. Observations were confined to Redshank feeding in an area of Seal Sands called Scalloped Mud (see Figure 4.1) which consists of medium to soft muds and remains exposed for 2-3 hours each side of low water. Observations were made from a 5m high slag wall along the southern edge of Scalloped mud.

4.2.2 Determination of race in the field

In order to identify the race of Redshank when observed in the field, Redshank were caught and colour-marked according to race using unique individual coloured ring combinations (n = 107 for *robusta;* n = 60 for *britannica*), leg flag combinations (n = 60 for *robusta;* n = 25 for *britannica*), and dye-marking combinations of contour feathers with picric acid (n = 22 for *robusta;* n = 11 for *britannica*).

Unfortunately, despite large numbers of birds being marked according to race, only small numbers of Redshank of known race were observed on any one day. This resulted from a large proportion of the birds marked in spring and autumn (when they were most easily caught) moving away from Seal Sands during mid-winter when numbers of Redshank were lowest. Those marked birds which did remain during winter were dispersed over the whole of Seal Sands when feeding, which

Figure 4.1: Seal Sands mud-flats showing Scalloped Mud where Redshank were observed foraging. ● invertebrate sampling positions (Evans, Ward & Mercer, 1996); ✕ position of heated taxidermic mount.



further limited the number of known race which could be observed feeding on Scalloped Mud.

4.2.3 Foraging Behaviour Observations

Observations of foraging behaviour of individual Redshank were made using a 20-60x 70mm zoom telescope from a vehicle which served as a mobile'hide'. Observations were confined to a period of 2h each side of LW during Spring tides (i.e. those tides with low water levels less than 1.3m OD) and were made on 2 days during each Spring tide every month, giving a total of 4 observation days per month.

Observations were confined to indiviuals foraging on open mud with a pace-peck motion and not with a scything side-to-side motion of the bill employed in water or very soft mud. The numbers of pecks and paces made by a foraging individual during each observation period were recorded on audio tape using a dictaphone. A 'peck' was defined as an attempt to take a prey item by probing or touching the surface of the sediment with the bill. Foraging rate was expressed by three parameters:

. Pecking Rate - the number of pecks made per minute.

. Pacing Rate - the number of paces taken per minute.

. Paces per Peck - pacing rate divided by pecking rate.

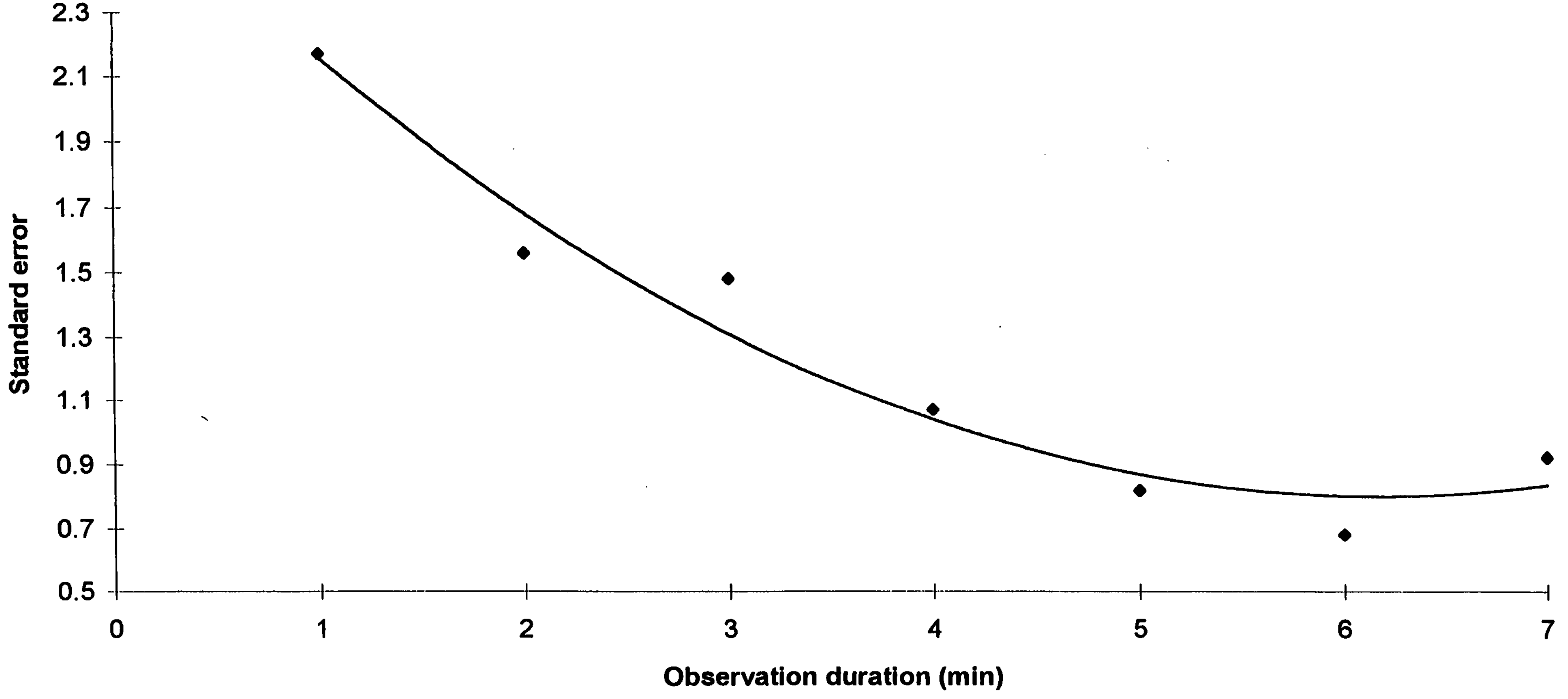
For the purposes of the present study, the measurement of foraging rates was thought to be sufficient to give an index of feeding effort and food intake for a large number of indiviuals throughout the winter season. Redshank react to visual cues during daylight when making a peck or probe into the substrate. A peck can therefore be a genuine attempt to capture prey in response to the perceived prescence of a prey item. Pecking rate is therefore an indicator of both prey density and feeding effort, though it is an over-estimate of food intake since not all pecks will be successful. Pacing rate and the number of paces per peck are indicators of prey density since the number of paces taken per minute (i.e. area of mud covered) is known to increase when prey is more sparsely distributed or less available (Goss-Custard, 1970; Speakman, 1983).

Additional behaviour was recorded and categorised as follows: i) Handling (i.e. manipulating a larger food item before swallowing), ii) Standing, iii) Roosting (i.e standing or sitting with eyes closed or head tucked under wing), iv) Preening, v) Vigilant (i.e alert posture with head held high, or head-bobbing, or crouched close to ground), and vi) Flight.

Individuals were observed for 5 minutes which proved to be the optimum observation time for minimising the standard error of mean pecking and pacing rates (measured in pecks and paces per minutes) of a group of 6 individuals observed during February 1993 (Figure 4.2). Time not spent pecking, pacing or handling prey was not included in the observation time. Observations taken over periods of less than 5 minutes were rejected from further analyses.

It was anticipated that the foraging behaviour of first year Redshank would differ from adults since the latter were significantly heavier throughout the winter (see chapter 2). Also, juveniles of many other bird species forage less efficiently than adults (e.g. see review: Marchetti & Price, 1989; Blackbird *Turdus merula*: Desrochers, 1992). Therefore, individuals which had juvenile-type plumage, characterised mainly by the patterns on tertials (Prater *et al.*, 1977) were not selected for observation. Cresswell & Whitfield (1994) demonstrated that age could be determined in the field by this method, even at distances of over 50m. Plumage differences between adult and first year Redshank become progressively less discernable throughout the winter; but the error resulting from the accidental

Figure 4.2: The effect of increasing observation duration on the standard error of the mean pecking rate of a sample of foraging Redshank (n=6) on 9 February 1993.



inclusion of occasional first years in the sample of birds observed was thought to be very small since few juveniles are present in winter at Teesmouth (Chapter 2).

4.2.4 Comparing diet composition of *britannica* and *robusta*

The Redshank in the present study fed predominantly on small prey items (<1mm). In preliminary studies it proved impossible to see consistently when a small prey item was taken by watching for a swallowing action (as was used in other studies at distances of up to 50m [e.g. Goss-Custard, 1969; Speakman, 1984]), but it has also proved difficult in other studies (e.g. Goss-Custard & Jones, 1976). Identification and quantification of prey items taken by observation of foraging Redshank was confined to larger items such as worms, bivalve molluscs and crabs. The numbers of large items seen to be taken have been shown, through gut analysis, to closely correspond with the numbers actually eaten (Goss-Custard, 1969).

Worms proved to be by far the most common large prey taken (see below). Because of the small numbers of individual Redshank of known race observed on any one day, convential statistical techniques were inappropriate to determine whether one race was taking more or less worms that the other. An alternative method was to determine whether the number of individuals of each race taking worms on a particular day deviated significantly from what would be expected from the proportions of all Redshank which were observed taking or not taking worms (see Appendix IV). This method is described by the example below:

On 6 March 1995 a total of 13 Redshank were observed, 10 birds took at least 1 worm in 5 minutes, 3 birds took 0 worms. Therefore, the probability P_1 that a bird from this sample will have taken a worm is 0.77, whilst the probability P_0 that a bird will not have taken a worm is 0.23. Of the 13 Redshank observed, 4 were known to be *robusta* and 3 were *britannica*; all had taken at least 1 worm. The probability of achieving the observation for each race based on the obervations from the whole sample is equal to : $(P_0)^{n_0} * (P_1)^{n_1}$ where n_0 is the number of birds of each race which had not taken worms and n_1 the number which had. Therefore, the probability of observing 4 *robusta* which had all taken worms is equal to: $(0.23)^0 * (0.77)^4 = 0.352$; and 3 *britannica* is $(0.23)^0 * (0.77)^3 = 0.457$. Since the probabilities calculated for of each race was greater than 0.05, the number of birds of each race taking worms was not significantly different from that day, as presented in Appendix IV.

However, if all 3 *britannica* observed on 6 March 1995 had not taken any worms but the rest of the birds observed had, the probability of this outcome would be $(0.23)^3 = 0.012$. It would therefore be concluded that *britannica* differed significantly from the other birds observed, in that they did not take any worms.

This technique considers only whether a bird fed on worms or did not, and does not consider the number of worms taken by an individual. The numbers taken in each 5 minute observation on a given day did not appear to follow either a poisson or normal distribution and thus, no realistic probabilities could be assigned to a particular number of worms taken; hence the binomial approach was used. The act of taking a worm appeared to be good indicator of an increase in preference for large prey compared with other times, given that on some days no indiviuals were observed to take worms , whilst on other days the majority of birds did so.

4.2.5 The effect of weather on foraging behaviour

Foraging rates were compared with measurements of windspeed and air temperature taken simultaneously with observations. Measurements of mean hourly windspeed (in m/s at 10m) and mean hourly air temperature (°C) were taken at Graythorp (data supplied by Hartlepool Borough Council) 2km from Seal Sands.

4.3 Results & Discussion

4.3.1 Foraging behaviour and race

In order to compare pecking rate, pacing rate and paces per peck between *robusta* (n=32 in 93/94; n=26 in 94/95) and *britannica* (n=41 in 93/94; n=33 in 94/95), the value of each parameter for a particular individual was subtracted from the relevant mean value for all Redshank on the same day (including those of unknown race) given in Appendix IV: Figure 1. There were no significant differences between races within both 1993/94 and 1994/95 in the deviations between individual and mean foraging parameters, which did not also deviate significantly from zero (Table 4.1).

4.3.2 Seasonal changes in foraging behaviour

In both races, pecking rate was significantly higher in 1993/94 than 1994/95, whilst the number of paces per peck was significantly lower in 1993/94 (Table 4.2). Pacing rate of *britannica* was significantly higher in 1994/95, though not significantly so in *robusta* (Table 4.2).

Despite both races showing apparent daily variation in pecking rate (Figure 4.3), pacing rate (Figure 4.4) and paces per peck (Figure 4.5), this variation was not significant (Kruskal Wallis test P>0.05). The lack of significance in daily variation in foraging was probably due to large individual variation coupled with small sample sizes, since daily variation was significant when all birds (including those of unknown race) were considered (see Appendix IV). The daily variation in pecking rates, pacing rates and paces per peck of of each race did appear to mirror those shown by all birds in Appendix IV. Indeed the daily median of at least one foraging parameter of each race in each winter was significantly correlated with the

Table 4.1: Comparison of mean differences between individual and population mean pecking rates, pacing rates and paces per peck of *robusta* and *britannica* Redshank during a) 1993/94 and b) 1994/95

a) 1993/94

	robusta **(n=32)** **mean ± 95%CI**	***britannica*** **(n=40)** **mean ± 95%CI**	t_{df}
pecking rate	-1.4±3.9	0.4±1.8	0.394_{44} ns
pacing rate	-0.7±5.7	-0.7±3.5	-0.01_{70} ns
paces per peck	-0.01±0.27	-0.01±0.14	0.02_{46} ns

b) 1994/95

	robusta **(n=26)** **mean ± 95%CI**	***britannica*** **(n=33)** **mean ± 95%CI**	t_{df}
pecking rate	2.1±2.2	0.0±1.9	1.45_{57} ns
pacing rate	-0.2±3.9	-1.3±3.7	0.42_{57} ns
paces per peck	-0.45±0.65	0.03±0.44	-1.26_{57} ns

Table 4.2: Kruskal-Wallis test statistics (χ^2_1) of variation due to year (i.e. 1993/94 or 1994/95) in pecking rate, pacing rate and paces per peck of *robusta* and *britannica* Redshank.

	britannica	***robusta***
Pecking rate	29.4***	28.7***
Pacing rate	11.7**	2.4 ns
Paces per peck	28.7***	22.0***

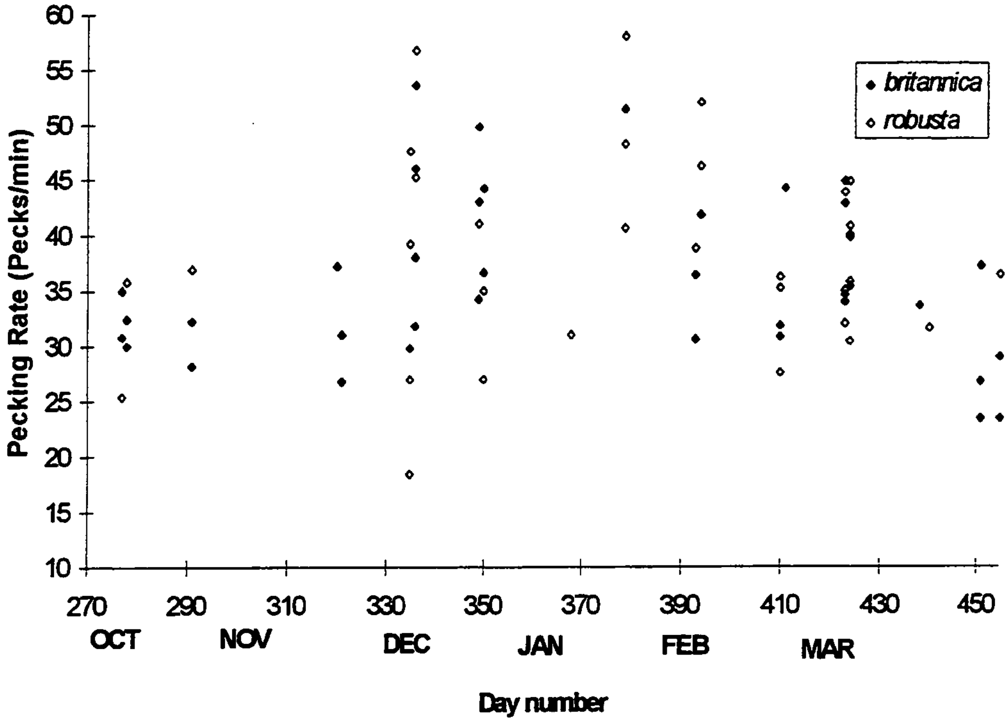
ns not significant i.e. $P>0.05$

** significance level of $P<0.001$

*** significance level of $P<0.0001$

Figure 4.3: Changes in pecking rate of *robusta* and *britannica* Redshank with day number during the winters of a) 1993/94 and b) 1994/95. (Day number 1 = 1 Jan 1993 or 1 Jan 1994 for the 1993/94 and 1994/95 winters respectively).

a) 1993/94



b) 1994/95

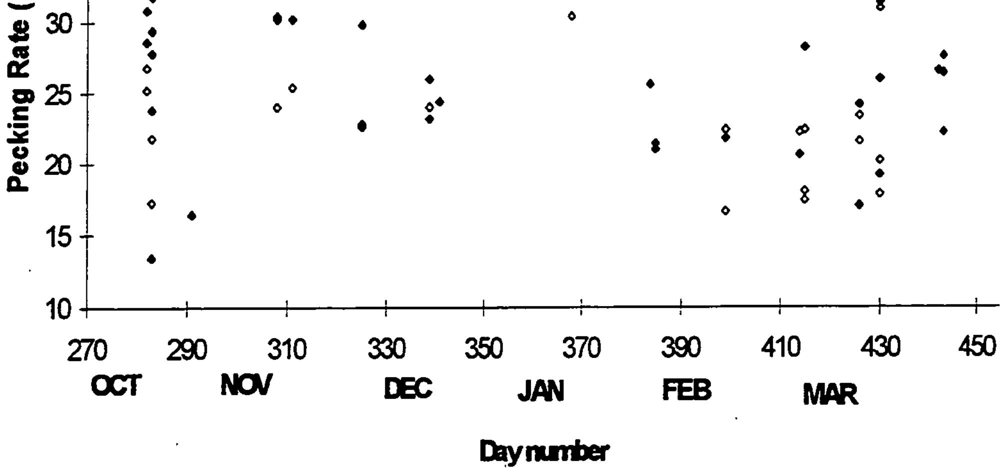
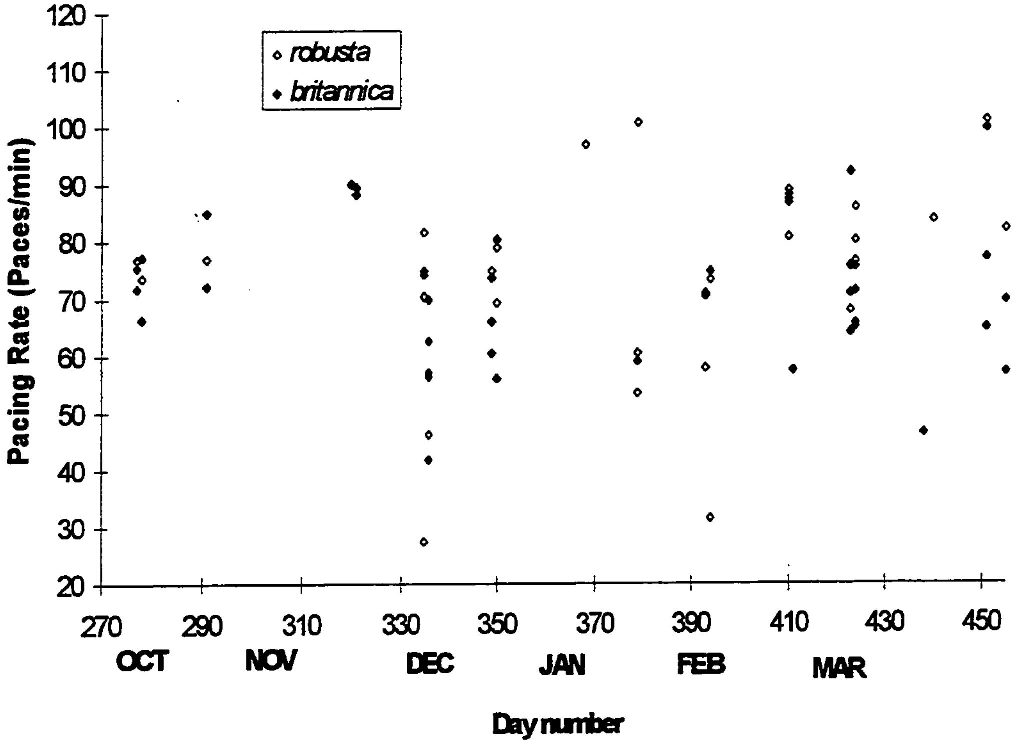


Figure 4.4: Changes in pacing rate of *robusta* and *britannica* Redshank with day number during the winters of a) 1993/94 and b) 1994/95. (Day number 1 = 1 Jan 1993 or 1 Jan 1994 for the 1993/94 and 1994/95 winters respectively).

a) 1993/94



b) 1994/95

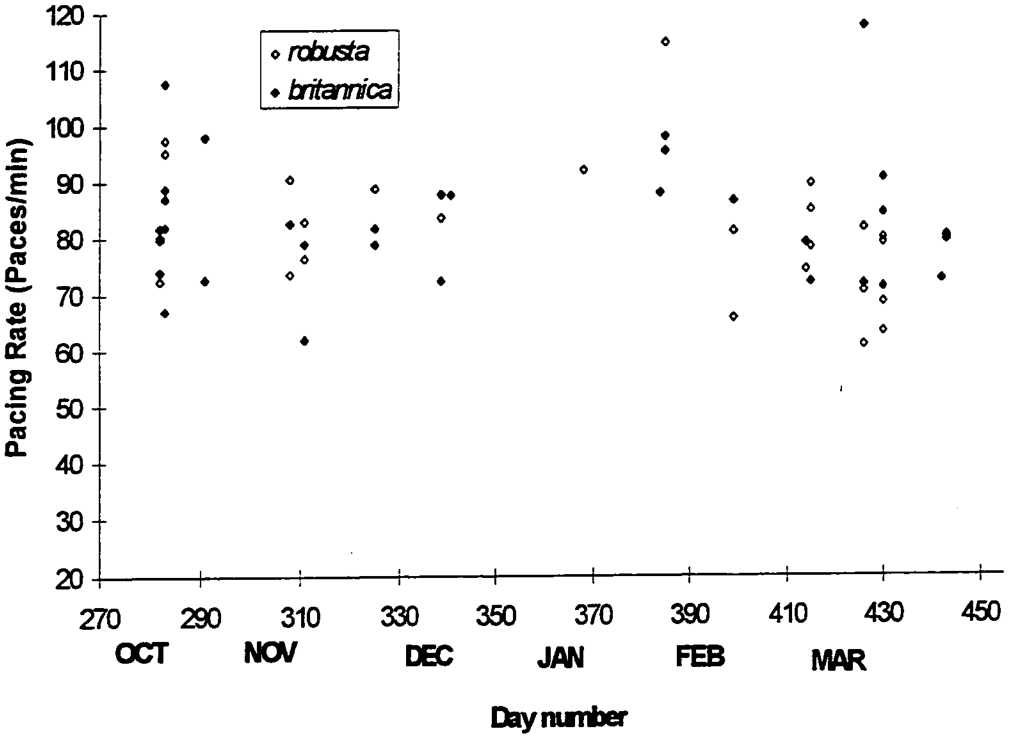
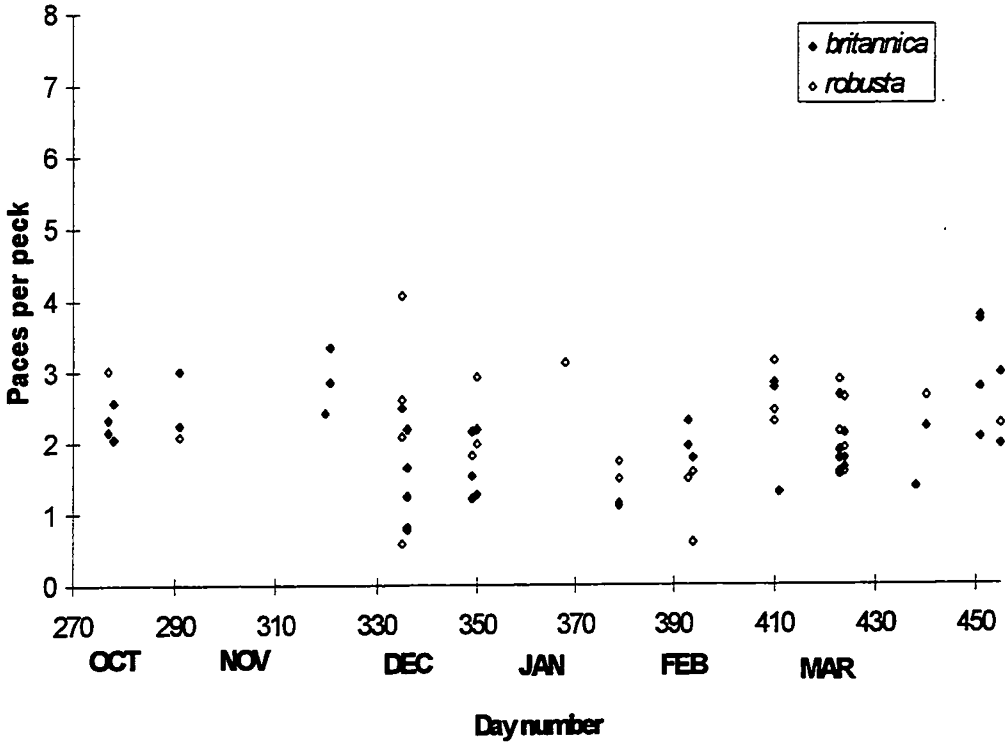
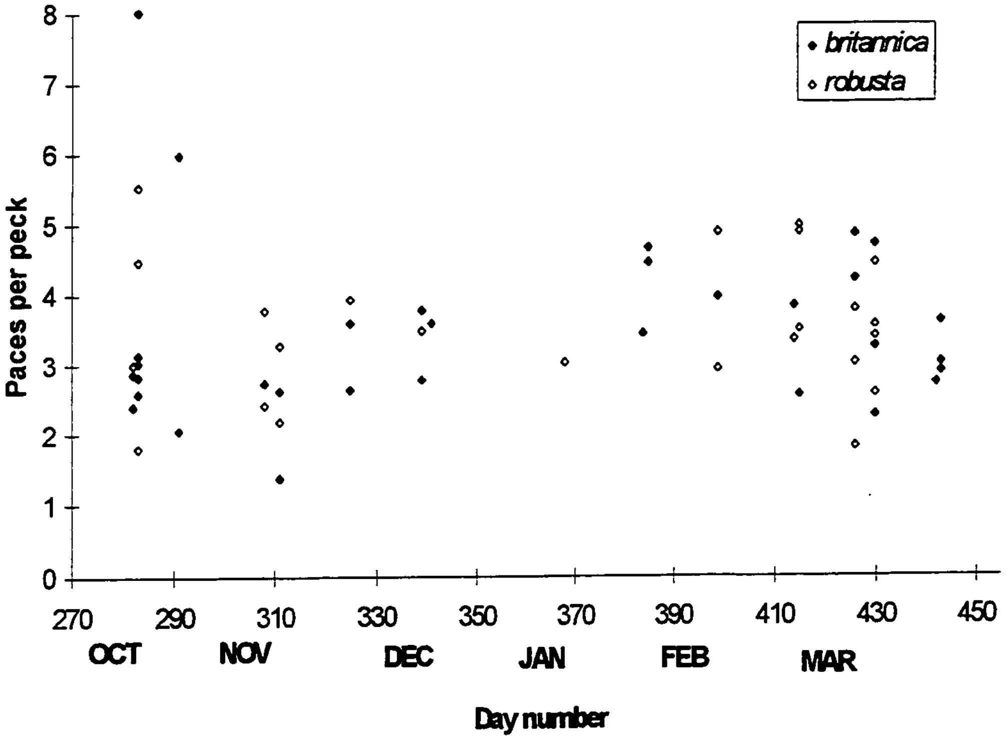


Figure 4.5: Changes in paces per peck of *robusta* and *britannica* Redshank with day number during the winters of a) 1993/94 and b) 1994/95. (Day number 1 = 1 Jan 1993 or 1 Jan 1994 for the 1993/94 and 1994/95 winters respectively).

a) 1993/94



b) 1994/95



daily mean of that parameter for all birds taken from Appendix IV (see Table 4.3 for correlation statistics).

In 1993/94 *britannica* showed significant monthly variation in both pecking rate and paces per peck (Kruskal-Wallis test $\chi^2_5 = 11.8$, $P<0.05$ for pecking rate; $\chi^2_5 = 13.7$, $P<0.05$ for paces per peck) but *robusta* did not.

4.3.3 The effect of ambient temperature and windspeed on foraging behaviour

Pecking rates, pacing rates and numbers of paces per peck were compared to mean hourly air temperature and wind speed at the time each observation was made. During the 1994/95 winter the pecking rate of *britannica* was positively correlated with air temperature but negatively correlated with wind speed and, since pacing rate was not correlated with windspeed, paces per peck rose significantly with windspeed (Table 4.4a). During 1994/95 the foraging behaviour of *robusta* was not correlated with air temperature, though pecking rate of *robusta* was negatively correlated with with wind speed (Table 4.4b).

The effects of air temperature and windspeed on the foraging of *britannica* and *robusta* were consistent with those described in Appendix IV for all the Redshank observed (including those of unknown race). The lack of significant correlation of air temperature with pacing rate and paces per peck of *britannica,* in contrast to the significant negative correlations shown by all birds (Appendix IV), was probably due to a small sample size (n=33 in *britannica* compared to n=184 for all Redshank) since the sign of r_s was the same in both groups. This was also true for *robusta* (n=26) for which no significant correlation was shown between air temperature and any foraging rate parameter.

Table 4.3: Spearman rank correlation coefficients r_s between daily median foraging parameters of a) *robusta* and b) *britannica* and daily mean foraging parameters of all Redshank shown in Appendix IV.

a) ***robusta***

	pecking rate	**pacing rate**	**paces per peck**
1993/94 (n=7)	0.714 ns	**0.893 ***	0.652 ns
1994/95 (n=8)	**0.935 ****	0.423 ns	**0.750 ***

b) ***britannica***

	pecking rate	**pacing rate**	**paces per peck**
1993/94 (n=13)	**0.623 ***	**0.762 ****	**0.787 ****
1994/95 (n=10)	0.469 ns	0.380 ns	**0.676 ***

ns	not significant i.e. $P>0.05$
*	significance level of $P<0.05$
**	significance level of $P<0.005$

Table 4.4: Spearman rank correlation coefficients r_s between foraging parameters and measurements of air temperature and wind speed taken at the time of foraging observations during the winter (Oct-Mar) of 1994/95 for a) *robusta* and b) *britannica* Redshank.

a) *robusta* (n=26)

	air temperature	**wind speed**
Pecking Rate	0.041 ns	-0.579 **
Pacing Rate	-0.076 ns	-0.371 ns
Paces per Peck	-0.002 ns	0.286 ns

b) *britannica* (n=33)

	air temperature	**wind speed**
Pecking Rate	0.344 *	-0.385 *
Pacing Rate	-0.134 ns	0.271 ns
Paces per Peck	-0.330 ns	0.386 *

ns	not significant i.e. P>0.05
*	significance level of P<0.05
**	significance level of P<0.01

The effects of weather on foraging behaviour in Redshank during the 1994/95 winter were consistent with existing theories on how weather can affect foraging behaviour, either directly or indirectly by altering prey density. The reduced pecking rate at low temperatures would indicate a lower detectability or availability of prey due to reduced activity of prey near the surface of the sediment (Goss-Custard, 1969; Evans, 1976; Pienkowski, 1983; Speakman, 1984). Consequently, searching effort (in terms of paces per peck) was greater at lower temperatures as the density of available prey decreased (Goss-Custard, 1970; Speakman, 1983). The reduced pacing and pecking rates observed at higher windspeeds on the open mudfats of Scalloped Mud confirm Davidson's (1981) suspicion that high winds hinder Redshank foraging, as shown in other long-legged shorebirds (Smith, 1975; Dugan *et al.*, 1981). Buffetting by high winds clearly interrupted the pacing rhythm of foraging Redshank and hence, reduced the area searched per unit time. The reduced area of mud searched may have caused the reduced pecking rate at high windspeeds because fewer prey were encountered. Additionally, high winds may have impaired the ability of the Redshank to detect visual cues indicating the prescence of prey; or may have enhanced drying of the surface of the sediment, possibly reducing prey activity (Evans, 1976).

In contrast to the 1994/95 winter, foraging behaviour of *robusta* and *britannica* during the 1993/94 winter was not significantly correlated with either air temperature or wind speed. The lack of significant correlations in both races during 1993/94 was unlikely to result solely from small sample sizes since when all birds were considered in Appendix IV, the only significant (negative) correlation was between pacing rate and air temperature.

The lack of correlation between foraging behaviour and weather conditions during 1993/94 compared to 1994/95, might have been explained by differences between the two winters in the conditions on the days that foraging observations were made. It may have been that the majority of observation days in 1993/94 had milder (i.e. higher air temperatures and lower wind speeds) and less varied weather conditions than those in 1994/95. Therefore in 1993/94, pecking rate for example, could be maintained at a higher and more constant level; hence no correlation between pecking rate and weather conditions would exist. However, these explanations can be dismissed, since overall, there was no significant difference between air temperature or wind speed during each observation in the two winters (Table 4.5).

4.3.4 Prey density and foraging behaviour

A more likely explanation for the differences in foraging behaviour of both races during the two winters is that prey density was higher during 1993/94. Figure 4.6 shows data taken from Evans *et al.* (1996) on densities of *Corophium volutator* measured from sediment cores taken in spring and autumn from 10 sampling stations on Scalloped Mud. The large variation in densities between sampling stations makes statistical comparisons between sampling periods difficult. However, Figure 4.6 clearly shows a marked and consistent decrease in densities of *Corophium* at all sampling stations between autumn 1993 and autumn 1994. Most intertidal benthos reproduces in summer and is therefore most abundant in autumn. Densities of *Corophium* fell from a maximum of $4775m^{-2}$ in autumn 1993 to no more than $99m^{-2}$ in autumn 1994 and were equally low in spring 1995. Goss-Custard (1977a) found that at high densities, *Corophium* was the preferred prey of Redshank. However, at densities of less than $300m^{-2}$, intake of *Corophium* decreased sharply and alternative prey were sought. Thus, the decrease in pecking rate and increase in paces per peck of both races in 1994/95 was probably caused by a marked reduction in the density of their preferred prey. It also appears that at high densities of *Corophium*, foraging rate is independant of prey behaviour under the range of weather conditions covered by this study. This milder (i.e. higher air temperatures and lower wind speeds) and less varied weather conditions than those in 1994/95. Therefore in 1993/94, pecking rate for example, could be maintained at a higher and more constant level; hence no correlation between pecking rate and weather conditions would exist. However, these explanations can be dismissed, since overall, there was no significant difference between air temperature or wind speed during each observation in the two winters (Table 4.5).

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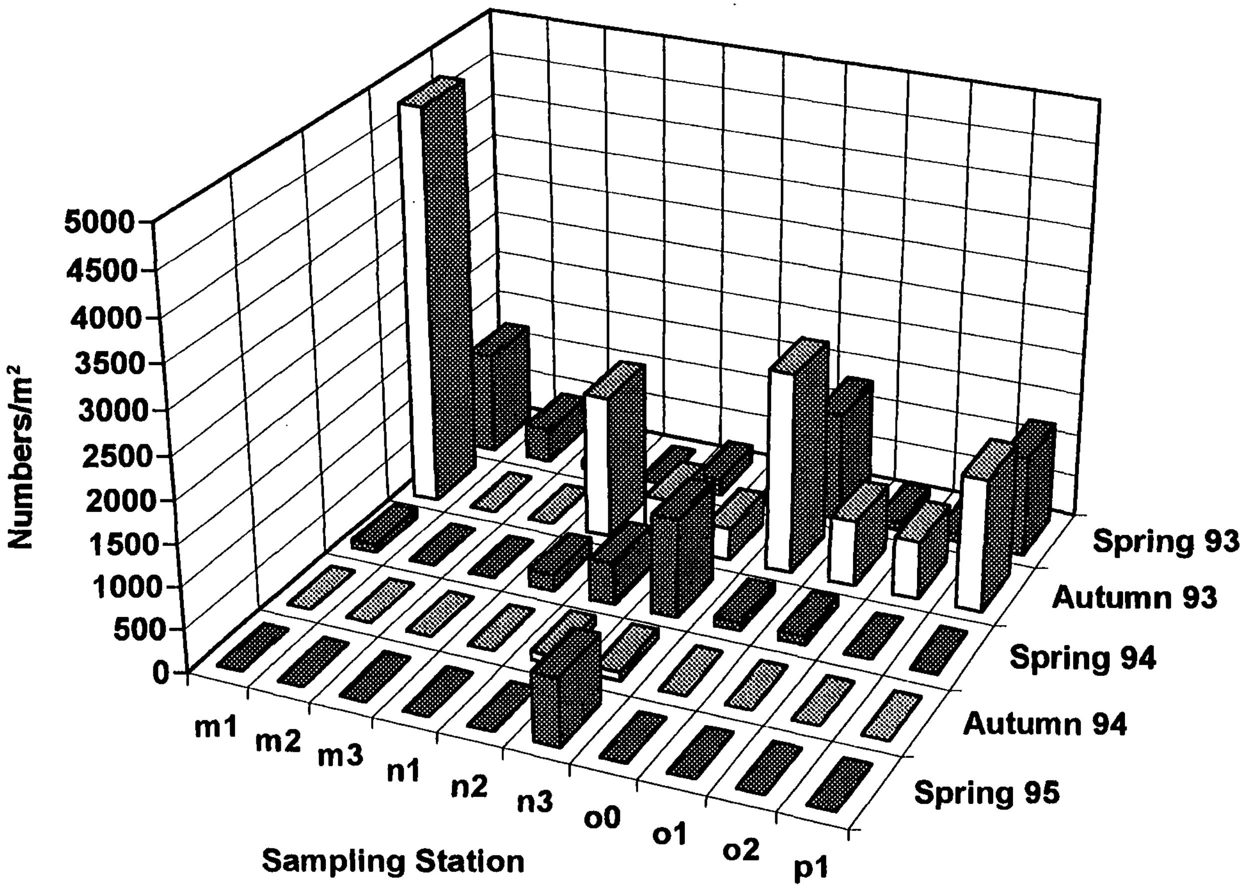
Table 4.5: Mean (in bold), SE (in parentheses), minimum and maximum air temperature, windspeed and M_{maint} during 5 minute foraging observation periods in 1993/94 (n=223) and 1994/95 (n=184).

	1993/94	1994/95	t
Air temperature (°C)	**6.3** (0.28) -2.6 - 14.1	**6.4** (0.33) -5.2 - 15.7	-0.20 ns
Wind speed (m/s)	**4.2** (0.13) 1.0 - 9.0	**3.8** (0.12) 0.5 - 7.1	[U=18876 ns]

Figure 4.6: Densities of *Corophium volutator* at sampling stations on Scalloped Mud, Teesmouth.



is not an unreasonable conclusion since Goss-Custard (1977a) found that intake rate of *Corophium* (under similar temperature conditions i.e mud temperature >6° C) was similar over a wide range of densities (around 300-5000+m^{-2}) at different sites.

The substantial decline in the densities of *Corophium* on Scalloped Mud may also have been accompanied by a decline in the density of the gastropod *Hydrobia ulvae*. Between autumn 1993 and autumn 1994, the densities of *Hydrobia* either decreased or remained below 99m^{-2} at 7 out of 10 sampling sites and the maximum density fell from 11,837 to 7,460m^{-2} (Figure 4.7). Goss-Custard (1977a) found that in areas where *Corophium* was absent, few small prey items (including *Hydrobia*) were taken; worms and other large items were taken instead. It appears therefore, that the density of *Hydrobia* would be relatively unimportant in affecting foraging behaviour, though proving this was beyond the scope of this study. The role of worms in the diet of Redshank at Seal Sands is discussed in Appendix IV.

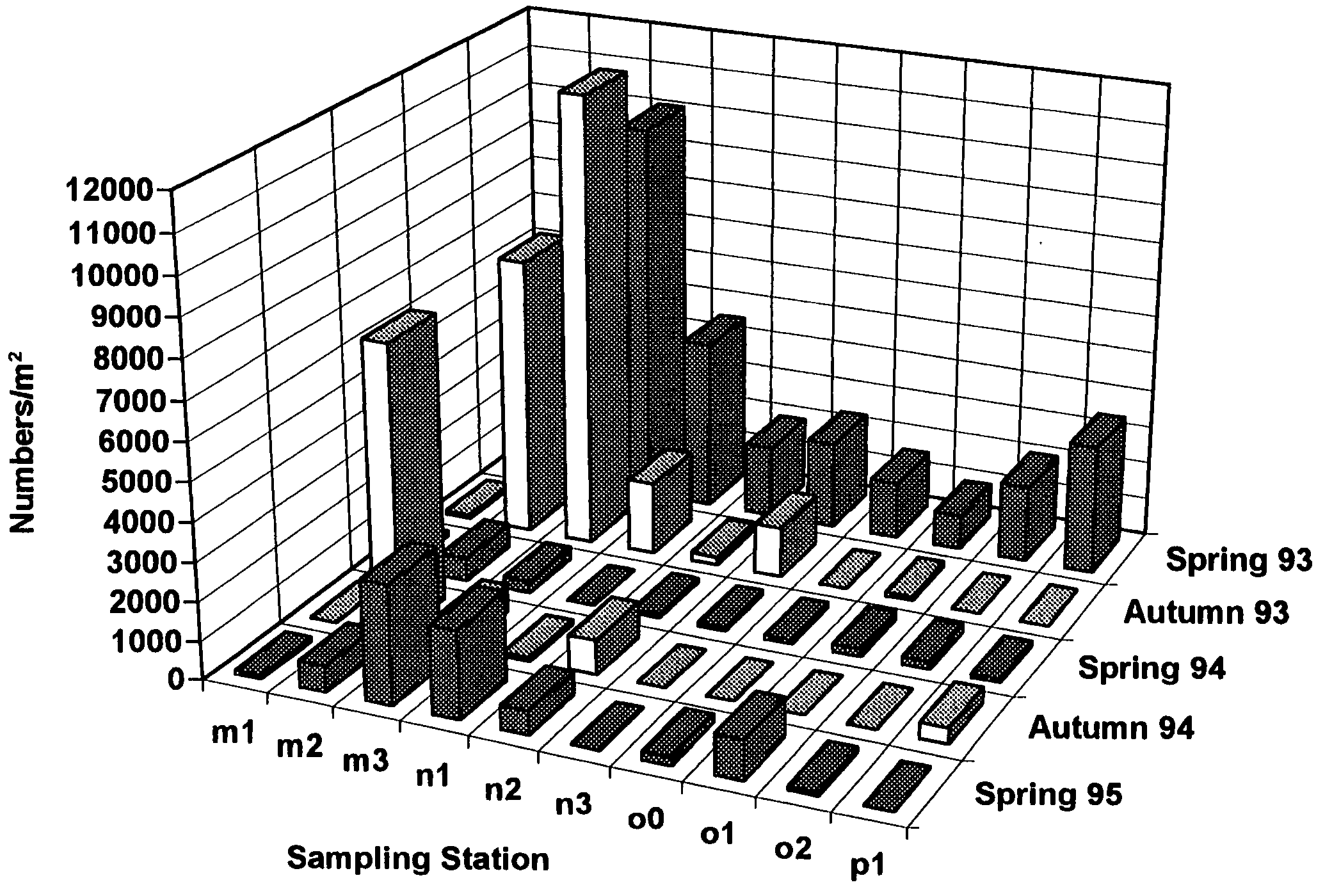
4.3.5 Numbers of larger prey items taken

For each day in both winters on which individuals of both races were observed, there was no significant difference ($P>0.05$) between the number of birds within a particular race and the number in the sample as a whole taking worms (see section 4.2.4).

4.3.6 Time Spent Foraging

The individuals which made up the Redshank flock at Seal Sands numbered between 120 and 620 in 1993/94 and 140 and 750 in 1994/95, and were synchronous in their activities. Whilst the majority were foraging, less than 10% were preening, roosting or standing. During the day (when this study was conducted) the majority of birds were foraging from at least 2 hours before MLWS

Figure 4.7: Densities of *Hydrobia ulvae* at sampling stations on Scalloped Mud, Teesmouth.



until between 2h and 4h 24min (1993/94) or between 2h 6min and 4h 13min (1994/95) after Low Water. There was no apparent difference between each of the two races and Redshank as a whole, in the way time was apportioned to separate activities. At any one time, the proportions of the individuals of a particular race assigned to a particular activity were not different from the proportion of the flock as a whole performing the same activity.

4.4 General Discussion

4.4.1 Racial differences in foraging

During this study, both races appear to have been equally capable of meeting their respective energy demands through foraging. Despite having a greater energy demand per unit body mass, *robusta* maintained a similar rate of foraging (which inferred a similar rate of intake) and foraged for similar periods to *britannica*. The *robusta* did not increase their energy intake by taking more energy-rich large worms. However, since small prey items (*Corophium* and *Hydrobia*) predominated in the diet, *robusta* might in fact have been selecting the larger size classes of prey such as *Corophium* and *Hydrobia*, though proving this was beyond the confines of this study.

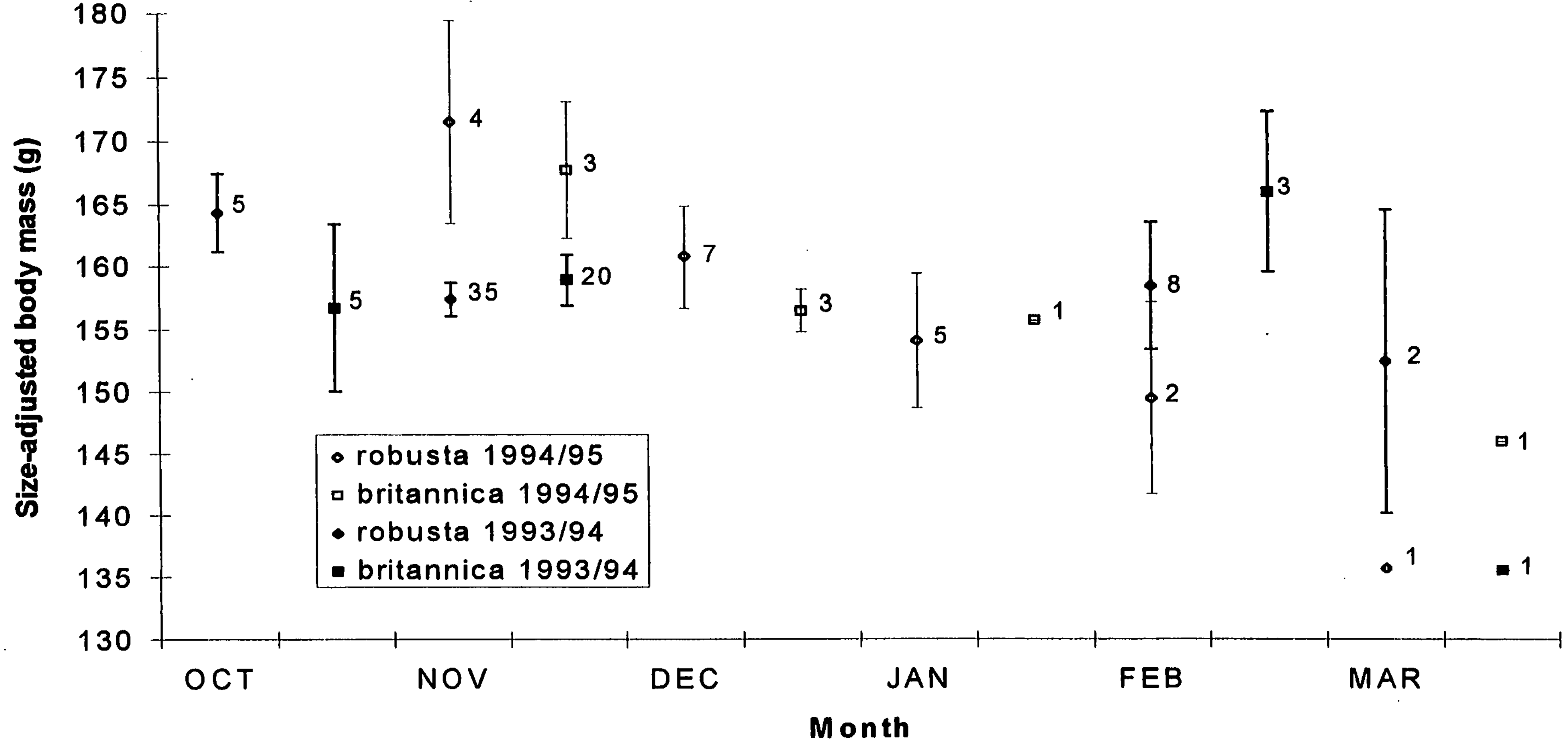
Observations during this study did not take place during prolonged periods of sub-zero temperatures, which were shown in Chapter 3 to seriously impair the ability of Redshank to maintain an energy balance. It may be that during such periods, *robusta* would have to increase their energy intake by making much more obvious changes in their foraging behaviour than could be detected during the mild conditions under which this study was conducted.

4.4.2 Consequences of changes in foraging behaviour on body mass

It might be expected that the lower pecking rate and consequently lower intake of small prey of both *robusta* and *britannica* in 1994/95 may have reduced their ability to regulate their body mass throughout the winter as described in chapter 2, and hence led to lower body masses than in the previous winter. Despite small sample sizes in 1994/95 Figure 4.8 shows that during November 1994 size-adjusted body mass BM′ of *robusta* was in fact significantly higher than during November 1993.($t_{30}=3.551$ $P<0.01$). Mean November BM′ of *britannica* also appeared to be higher in 1994 than in 1993, but was not significantly so. November BM′ of *robusta* was not significantly different from that of *britannica* during both 1993 and 1994.

A possible explanation of higher body mass in November 1994 (when prey density was apparently lower than in the previous November) is that Redshank in 1994 were responding to the low density of *Corophium* by building up more fat stores in early winter as insurance against unpredictable food intake during the rest of the winter. This explanation follows Lima's (1986) model which predicted that birds faced with less predictable food supply during winter would accumulate more insurance fat than those with more predictable food sources given that predation risk was the same in both cases. Certainly, the differences between the foraging responses of *robusta* and *britannica,* and of Redshank as a whole (Appendix IV) to weather during 1993/94 and 1994/95 suggest that food intake and the ability to satisfy energy demand was less predictable in 1994/95. Due to insufficient data it is unclear whether the insurance fat accumulated in November 1994 was sufficient to maintain 'normal' body mass later in that winter.

Figure 4.8: Mean monthly size adjusted body mass of *robusta* and *britannica* during 1993/93 and 1994/95. Error bars indicate 2xSE and numbers denote sample size.



5.0 Mobilisation of body reserves during severe weather

5.1 Introduction

The aim of this chapter is to determine the extent to which body reserves of *robusta* and *britannica* are mobilised prior to death following periods of severe weather. In doing so, I will determine the most likely cause of death (i.e. i) starvation, or ii) an inability to mobilise reserves fast enough to meet immediate energy demands) in each race following severe weather. By combining information on levels of fat and protein reserves by the two races at death with levels of reserves carried during 'normal' winter weather (Chapter 2), it will be possible to determine the amount of reserves that are actually available for mobilisation when energy intake from food is insufficient to satisfy high energy demands for maintenance during severe weather. Hence, by combining knowledge of the energy available in reserve and the levels of energy expenditure (Chapter 3), one can estimate the expected survival times of each race, assuming that all energy is being derived from body reserves. The expected survival times of each race will give an indication of their potential to survive through periods when maintenance costs are high and energy intake from food is likely to be relatively low.

This chapter will present information on the body composition of both races of Redshank which died on the Wash following severe weather in February 1991. Unusually for such events the time at which mortality began is known with reasonable confidence, around 10 February given the state of corpses which were first found on 17 February (Clark *et al.*, 1993). The time at which mortality started during February 1991 is more definite at Teesmouth, where the first Redshank corpses were recovered on 12 February (pers. comm. R. M. Ward). Therefore, the energy expenditure prior to death at Teesmouth and the Wash was modelled using the predictive models for M_{maint} formulated in Chapter 3. By comparing between races, the proportion of total energy expenditure prior to death which was supplied by the catabolism of body reserves and by the assimilation of food, it is hoped to determine which race is more vulnerable during severe weather.

5.2 Methods

5.2.1 Carcass Analysis

Those corpses which were analysed during this study were collected from the Wash shoreline at Terrington, Thornham and the eastern Wash on 16 and 17 February 1991. On the day of collection, each intact corpse was aged according to plumage characteristics (Prater *et al.,* 1977) and sexed by dissection. Measurements were taken of wing-length (maximum chord) to 1mm using a stopped rule, bill-length to 0.1mm using vernier callipers and tarsus-toe to 1mm using a stopped rule (see Clark *et al.*, 1993). The discriminate function formula of Summers *et al.* (1988) was applied to measurements of wing-length, bill-length and tarsus-toe in order to predict racial origin. The corpses were then deep-frozen together.

In June 1994, a sample of Redshank corpses were obtained by permission from N. A. Clark and J. A. Clark of the British Trust for Ornithology. The corpses were partially defrosted to enable the separation of each corpse which was then individually sealed in polythene bags and re-frozen.

A total of 59 carcasses were destructively analysed, of which 31 were identified as *robusta* (16 females and 15 males) and 28 as *britannica* (13 females and 15 males). Each corpse was defrosted and then weighed to the nearest mg on a torsion balance. The liver and left pectoral muscle block (consisting of *pectoralis major* and *supracoracoideus*) were dissected out and weighed to the nearest mg. Four skeletal measurements of the area of attachment were taken to 0.1mm using vernier callipers as shown in Piersma *et al.* (1984) to estimate the by the catabolism of body reserves and by the assimilation of food, it is hoped to determine which race is more vulnerable during severe weather.

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5.2.1 Carcass Analysis

Those corpses which were analysed during this study were collected from the Wash shoreline at Terrington, Thornham and the eastern Wash on 16 and 17 February 1991. On the day of collection, each intact corpse was aged according to plumage characteristics (Prater *et al.*, 1977) and sexed by dissection. Measurements were taken of wing-length (maximum chord) to 1mm using a stopped rule, bill-length to 0.1mm using vernier callipers and tarsus-toe to 1mm using a stopped rule (see Clark *et al.*, 1993). The discriminate function formula of Summers *et al.* (1988) was applied to measurements of wing-length, bill-length and tarsus-toe in order to predict racial origin. The corpses were then deep-frozen together.

In June 1994, a sample of Redshank corpses were obtained by permission from N. A. Clark and J. A. Clark of the British Trust for Ornithology. The corpses were partially defrosted to enable the separation of each corpse which was then individually sealed in polythene bags and re-frozen.

A total of 59 carcasses were destructively analysed, of which 31 were identified as *robusta* (16 females and 15 males) and 28 as *britannica* (13 females and 15 males). Each corpse was defrosted and then weighed to the nearest mg on a torsion balance. The liver and left pectoral muscle block (consisting of *pectoralis major* and *supracoracoideus*) were dissected out and weighed to the nearest mg. Four skeletal measurements of the area of attachment were taken to 0.1mm using vernier callipers as shown in Piersma, Davidson & Evans (1984) to estimate the standard muscle volume SMV. SMV is an estimation of the space in the thorax which could potentially be occupied by the pectoral muscles and is used to standardise measurements of muscle mass (see below).

The dissected carcass, pectoral muscle and liver were dried to constant mass at 40°C in a vacuum oven. Storage lipids (triglycerides), were extracted from the dissected carcass, pectoral muscle and liver using a Sohxlet extractor and petroleum ether as a solvent. The liver and pectoral muscle were ground in a pestle & mortar prior to extraction. The fat-free carcass, pectoral muscle and liver were dried to constant mass at 40°C in a vacuum oven.

Table 5.1 lists abbreviations and definitions of parameters of body composition used in this study.

Body size S was calculated for each carcass from equation 2.1 (Section 2.2.2) incorporating measurements of wing-length, bill-length and tarsus-toe. BM, TDBM TLM and TLDM of each carcass were adjusted for body size in a similar way to that used to adjust BM and PTLM of live wild Redshank in Sections 2.2.2 and 2.2.5 respectively. The regressions of BM, TDBM, TLM and TLDM with S are given below in equations 5.1-5.4.

$$\mathrm{BM} = (S * 1.34) - 113.8 \qquad n = 58 \quad R^2 = 0.16 \qquad P<0.002 \qquad \mathbf{5.1}$$

$$\mathrm{TDBM} = (S * 0.58) - 58.7 \qquad n = 59 \quad R^2 = 0.21 \qquad P<0.001 \qquad \mathbf{5.2}$$

$$\mathrm{TLM} = (S * 1.38) - 122.1 \qquad n = 52 \quad R^2 = 0.24 \qquad P<0.001 \qquad \mathbf{5.3}$$

$$\mathrm{TLDM} = (S * 0.44) - 37.9 \qquad n = 52 \quad R^2 = 0.37 \qquad P<0.0001 \qquad \mathbf{5.4}$$

The regressions in equations 5.1-5.4 are based on all carcasses since there was no significant difference between the slopes or intercepts of each regression when carcasses of the two races were treated separately (MANOVA $P>0.05$). The slope

Table 5.1: Abbreviations and definitions of body composition parameters

Abbreviation	Definition
BM	total body mass
TDBM	total dry body mass
TLDM	total lean (after lipid extraction) dry mass
FM	mass of total extractable fat = (TDBM - TLDM)
TLM	total lean mass = (TBM - TFM)
LI	Lipid Index = ((TFM/TBM)*100)
DLI	dry lipid index = ((TFM/TDBM)*100)
WATER	percentage water content = ((TBM-TDBM/TLM)*100)
MUSLDM	lean dry mass of one pectoral muscle block
SMV	standard muscle volume
SMI	standard muscle index = (MUSLDM/SMV)
MI	muscle index = ((2*MUSLDM)/TLM)*100)
LIVLDM	lean dry mass of liver
LIVI	liver index = ((LIVLDM/TLDM)*100)
MUSLI	muscle lipid index = (mass of extractable lipid of one pectoral muscle block)/(lean mass of one pectoral muscle block)
LIVLI	liver lipid index = (mass of extractable lipid of liver)/(lean mass of liver)

of each of equations 5.1-5.4 were then used to create the adjustment terms bm, tdbm, tlm and tldm respectively in equations 5.5-5.8:

$$bm = 1.34 * S_d \qquad \textbf{5.5}$$

$$tdbm = 0.58 * S_d \qquad \textbf{5.6}$$

$$tlm = 1.38 * S_d \qquad \textbf{5.7}$$

$$tldm = 0.44 * S_d \qquad \textbf{5.8}$$

where $S_d = S' - S$; where $S' = 160.5$ which was the mean value of S in 633 wild adult Redshank at Teesmouth (see section 2.2.2).

Size-adjusted body mass BM'_d, dry body mass $TDBM'_d$, total lean mass TLM'_d and total lean dry mass $TLDM'_d$ at death were calculated as:

$$BM'_d = BM + bm \qquad \textbf{5.9}$$

$$TDBM'_d = TDBM + tdbm \qquad \textbf{5.10}$$

$$TLM'_d = TLM + tlm \qquad \textbf{5.11}$$

$$TLDM'_d = TLDM + tldm \qquad \textbf{5.12}$$

Therefore, the size-adjusted mass of fat at death FM'_d was calculated as:

$$FM'_d = TDBM'_d - TLDM'_d \qquad \textbf{5.13}$$

5.2.2 Estimation of the size of available reserves

Mean size-adjusted body mass BM′ and total lean mass PTLM′ (predicted using TOBEC) of live wild *robusta* and *britannica* at Teesmouth during January (taken from Chapter 2) were used as estimates of ‘normal’ body mass BM'_n and lean mass $PTLM'_n$ of both races of equal size S = 160.5, prior to the onset of severe weather at the beginning of February 1991. The mass of fat FM'_n of a Redshank of each race and of S=160.5, was calculated as BM'_n minus $PTLM'_n$. The mass of fat reserve available for catabolism FM'_R in Redshank of each race of S=160.5 was calculated as:

$$FM'_R = FM'_n - FM'_d \qquad 5.14$$

The mass of protein available for catabolism LDM'_R in Redshank of each race of S=160.5 was calculated as:

$$LDM'_R = PLDM'_n - TLDM'_d \qquad 5.15$$

where $PLDM'_n$ is an estimation of lean dry mass of live Redshank of S=160.5 prior to the onset of severe weather in February 1991, calculated as :

$$PLDM'_n = 0.33 * PTLM'_n \qquad 5.16$$

where 0.33 is the proportion of lean dry mass to fresh lean mass of Redshank in 'normal' condition (I. Scott, unpubl. data), i.e. 67% of lean mass is water.

The total amount of energy E_{res} available for assimilation of fat and protein reserves in a Redshank of either race of S=160.5 was calculated as:

$$E_{res} = (17.99 * LDM'_R) + (39.33 * FM'_R) \qquad 5.17$$

where 17.99 and 39.33 are the energy values in KJ/g of protein and fat respectively (Schmidt-Nielsen, 1984).

5.2.3 Estimation of Survival time

The period of 6 - 14 February 1991 was, for the purposes of this study, considered to have been severe and necessitated the use of body reserves to supplement the energy intake from feeding. The period of 6 - 14 February 1991 was defined as severe because on each day, the daily total M_{maint} of each race exceeded 2.5xBMR (see Chapter 3) and mean daily air temperature was below 0°C. The length of time T (days) for which a Redshank of either race could survive on the energy assimilated from fat and protein reserves alone was calculated as:

$$T = E_{tot} / E_{res} \qquad \textbf{5.18}$$

where E_{tot} is the total daily energy expenditure in KJ, estimated by adding an activity cost of 1.5xBMR to estimated daily M_{maint}.(see chapter 3) for a Redshank of BM′= 152.1g and of BM′ = 156.2g, the mean values for *britannica* and *robusta* respectively during January at Teesmouth (Chapter 2).

5.3 Results

5.3.1 Body composition at death

Table 5.2 shows a comparison of all body composition parameters at death between *robusta* and *britannica*. BM, TDBM, TLM and TLDM were all significantly greater in *robusta* corpses. However, *robusta* were significantly larger in body size S and the size-adjusted parameters BM'_d, $TDBM'_d$, TLM'_d and $TLDM'_d$ were not significantly different between the two races.

The pectoral muscles had almost halved in size compared to presumed typical measurements of SMI and MI of 0.176(±0.49) and 4.2%(±0.6) respectively taken from Redshank during a 'mild' February at Teesmouth by Davidson (1981a). Despite having the same total fresh and dry lean masses when adjusted for body size, the mass of pectoral muscle relative to body size (measured by SMI and MI) was significantly larger in corpses of *britannica* (Table 5.2). The differences in SMI and MI were purely racial, since neither SMI or MI was significantly

Table 5.2: Composition of corpses of *robusta* and *britannica* collected from the Wash following severe weather in February 1991. * indicates t-test was performed on arcsine-transformed percentages

	robusta		***britannica***		t_{df}	**P**
	mean±95%CI	n	mean±95%CI	n		
BM g	107.9±5.9	30	97.9±4.5	28	2.75_{56}	**0.008**
TDBM g	37.3±2.3	31	32.6±1.3	28	3.54_{57}	**0.001**
TLM g	104.3±5.4	26	95.9±4.3	26	2.50_{50}	**0.016**
TLDM g	34.7±1.1	26	31.5±1.2	26	4.04_{50}	**<0.001**
WATER %	66.4±1.3	26	67.1±0.9	26	0.86_{50}*	0.394
FM g	0.81±0.15	26	1.01±0.24	26	1.46_{50}	0.150
LI %	0.79±0.15	26	1.01±0.20	26	1.81_{50}*	0.076
DLI %	2.29±0.41	26	3.01±0.59	26	1.98_{50}*	0.053
MUSLDM g	1.258±0.114	28	1.344±0.104	28	1.14_{57}	0.261
SMI	0.072±0.007	28	0.086±0.008	28	2.52_{57}	**0.015**
MI %	2.37±0.24	26	2.78±0.25	26	2.52_{50}*	**0.015**
LIVLDM g	0.492±0.045	26	0.461±0.049	26	0.97_{56}	0.334
LIVI %	1.41±0.12	26	1.45±0.15	28	0.41_{50}*	0.680
MUSLI %	1.21±0.54	28	1.09±0.34	28	0.28_{57}*	0.782
LIVLI %	2.99±0.19	28	3.39±0.41	28	1.75_{41}*	0.093
S	164.6±1.0	28	158.1±1.2	28	8.36_{57}	**<0.001**
BM$'_d$ **g**	102.6±5.9	28	101.2±3.8	28	0.400_{56}	0.693
TDBM$'_d$ **g**	35.0±2.2	28	34.0±1.2	28	0.72_{45}	0.462
TLM$'_d$ **g**	98.6±5.1	26	99.6±3.7	26	-0.32_{50}	0.748
TLDM$'_d$ **g**	32.9±1.0	26	32.6±1.1	26	0.31_{50}	0.758
FM$'_d$	0.23±0.20	26	1.38±0.24	26	7.30_{50}	**<0.001**

correlated with S within each race. The lean mass of liver and LIVIN were similar in corpses of both races.

Fat reserves were almost completely depleted, with around 1g or 1% (LI) remaining in both races. LI and DLI were slightly higher in *britannica* corpses, though not significantly so (Table 2.2). The relative amounts of fat in pectoral muscle (MUSLI) and liver (LIVLI) were similar in both races. However, for a bird of size S=160.5, the mass of fat remaining at death FM'_d was significantly larger in *britannica*. Absolute and relative fat levels were similar in both male and female *robusta;* however, Table 5.3 shows significant differences in fat levels in corpses of male and female *britannica*. Female *britannica* died with significantly higher FM, LI, DLI and MUSLI than male *britannica*. These differences in lipid levels between male and female *britannica* appeared to result from females being larger in body size than males, since, even though there was no significant difference in S between the sexes, FM'_d was not significantly larger in females. Fat content of the liver (LIVLI) of *britannica* was similar in both sexes.

5.3.2 Estimated survival time

Table 5.4 shows how an individual of each race but of equal body size had very similar energy reserves to mobilise during periods of negative energy balance in February 1991. However, the lower M_{maint} of *britannica* meant that it could survive purely on its fat and protein reserves for half a day longer than *robusta* at both the Wash and Teesmouth.

Table 5.3: Parameters of body size and lipid content in corpses of male and female *britannica* collected from the Wash in February 1991.

	female		male		t_{df}	P
	mean±95% CI	n	mean±95% CI	n		
S	158.7±1.3	13	157.5±2.1	15	-1.09_{26}	(0.285)
FM g	1.26±0.19	13	0.75±0.09	15	2.42_{24}	**0.024**
LI %	1.22±0.16	13	0.80±0.08	15	2.28_{24}*	**0.032**
FM'_d	1.51±0.40	13	1.25±0.28	15	0.30_{24}	(0.242)
DLI %	3.62±0.45	13	2.39±0.27	15	2.21_{24}*	**0.037**
MUSLI %	1.47±0.33	13	0.75±0.06	15	2.99_{26}*	**0.006**
LIVLI %	3.58±0.30	13	3.24±0.27	15	0.96_{28}*	(0.348)

* t-test performed on arcsine-transformed percentages

Table 5.4: Estimated energy reserves and survival time of *robusta* and *britannica* adjusted to an equal body size S=160.5.

	britannica	***robusta***
$PLDM'_n$	45.3g	44.4g
$PTLM'_d$	32.6g	32.9g
LDM'_R	**12.7g**	**17.5g**
	228KJ	**207KJ**
PFM'_n	19.0g	17.7g
FM'_d	1.4g	0.2g
FM'_R	**17.6g**	**17.5g**
	692KJ	**688KJ**
E_{res}	**921KJ**	**895KJ**
Mean daily E_{tot} on the Wash	**357KJ/d**	**424KJ/d**
Estimated survival time T on the Wash	**2.6days**	**2.1days**
Mean daily E_{tot} at Teesmouth	**341KJ/d**	**405KJ/d**
Estimated survival time T at Teesmouth	**2.7days**	**2.2days**

5.4 Discussion

5.4.1 Body composition at death

Both races died with around 1% (LI) of extractable fat remaining at death, which is consistent with other studies of Redshank (Davidson & Evans, 1982) and of other species (e.g. Marcstrom & Mascher, 1978 on Lapwing (*Vanellus* vanellus) and Oystercatcher; Piersma *et al.*, In Press on Knot and Oystercatcher) in which the composition of birds which had died following severe weather was analysed. The remaining 1% of fat at death has been termed 'structural lipid' by some authors (e.g. Davidson & Evans, 1982; Piersma *et al.*, In Press) which would imply that this residual fat is composed of phospholipids rather than storage lipids (i.e. triglycerides). However, the studies mentioned above all used petroleum ether as an extraction solvent which only removes triglycerides and not phospholipids (Blem, 1990). It is therefore inaccurate to describe the residual 1% of extractable fat as 'structural', since it is actually storage lipid which could not be mobilised.

The extensive use of breast muscle and other lean tissue by Redshank of both races is consistent with other studies, in which the birds analysed were believed to have died of starvation (Marcstrom & Mascher, 1978; Visser, 1978; Davidson & Evans, 1982; Davidson & Clark, 1985b; Clark & Davidson, 1986; Piersma *et al.*, In Press), rather than an inability to mobilise reserves fast enough to satisfy immediate energy demands (Davidson & Clark, 1985b). The fact that both races had almost depleted their fat reserves and substantially used protein reserves is consistent with what would be expected in fasting birds which mobilise available lipid reserves before catabolising protein (Le Maho, 1983; Cherel & Le Maho, 1985). The utilisation of pectoral muscle protein indicated that both races had reached a point whereby further catabolism of protein would be structurally damaging. It appears from my comparison of body composition in wild and captive Redshank (Chapter

2) that protein in the liver and alimentary canal can be catabolised more readily and with less fitness costs than muscle protein.

Both races of Redshank died with the same amounts of lean tissue relative to body size, though slightly more fat and proportionately larger pectoral muscles remained in *britannica*. Piersma *et al.* (In Press) demonstrated that individuals within a species of shorebird (Knot, Dunlin and Oystercatcher) which appeared to have higher overall energy demands prior to death from starvation, died with a higher mass of lean tissues. Likewise, Davidson & Evans (1982) found that Redshank which died following severely low temperatures in Montrose, Scotland in January 1982 had consistently higher BM, TLM, MI and significantly higher LI than Redshank which died following slightly warmer but windier conditions in 1979 on the Ythan Estuary. Piersma *et al.* (In Press) reasoned that birds died when the overall energy output from the metabolically active lean tissues was lower than that required for maintenance. They argued that therefore, individuals which needed to produce large amounts of energy for M_{maint} required a larger lean mass to do so and therefore died with a larger lean mass than individuals with the same output per gram of tissue but a lower demand for M_{maint}. In my study, *robusta* had a higher M_{maint} than *britannica* before dying in February 1991 (Table 5.4) but the output from the tissues (i.e. mass-specific BMR) of *robusta* was also higher (Chapter 3) by the same amount (i.e. at a particular T_{es}, M_{maint} of each race amounts to the same multiple of their respective BMR's: Chapter 3). Therefore, individual *robusta* and *britannica* of the same body size could satisfy their respective demands for M_{maint} with the same mass of lean tissue and consequently died of starvation with the same mass of lean tissue remaining.

The significantly larger SMI and FM'_d in *britannica* at death may have been due to a difference in physiology between the two races, in that more storage lipid and proportionately more pectoral muscle protein were available for mobilisation in *britannica*. Alternatively, since *britannica* could survive for longer on their reserves, the majority of *britannica* which died may have done so after conditions which required slightly more energy for M_{maint}. Indeed, mean daily air temperatures were lowest at the end of the severe period (Figure 5.1).

5.4.2 Implications of survival time of *robusta* and *britannica*

Both *robusta* and *britannica* had similar sized energy reserves to draw from during the severe weather in February 1991, but daily energy expenditure was higher in *robusta* which therefore needed to assimilate more energy from food compared to *britannica* which could survive on their reserves alone for half a day longer. It would appear then, that *robusta* were under-insured in terms of the amounts of fat and protein which were accumulated in winter. Piersma *et al.* (In Press) found that northerly wintering Knot were under-insured compared to Knot wintering in west Africa, since although the latter carried smaller reserves, they could survive on them alone for longer since costs of M_{maint} were much lower. Both these instances of apparent under-insurance lend additional support for the thinking that increasing body mass in mid-winter has a cost (Witter & Cuthill, 1993) and consequently that the costs are traded-off against the potential advantages of carrying insurance reserves (Lima, 1986).

Estimated survival times when satisfying mean daily energy costs only by the mobilisation of reserves between 6-14 February 1991 were 2.6-2.7 days for *britannica* and 2.1-2.2 days for *robusta*. Since the earliest day that Redshank started to die was probably 10 February on the Wash and certainly 12 February at Teesmouth, at least 1.4-3.4 (*britannica*) and 2.1-4.1 (*robusta*) days worth of the total energy requirements up until death must have been satisfied by the assimilation of food. Table 5.5. illustrates that the energy required from food per day during 6-14 February 1991 at Teesmouth was up to 80% and 76% of E_{tot} in *robusta* and *britannica* respectively during 'mild' conditions in February 1983 and

1984. Sub-zero temperatures during February 1991 (Figure 5.1 and Table 5.5) must have had a detrimental effect on food intake (see Chapter 4) at Teesmouth. Even lower temperatures and higher wind speeds (Figure 5.1 and Table 5.5) probably further reduced food intake on the Wash during February 1991 and may have been responsible for the apparently earlier start of mortality on the Wash compared to Teesmouth. At both sites during February 1991 *robusta* had to obtain a higher percentage of 'normal' E_{tot} from food than *britannica*, in addition to requiring absolutely more energy from food assimilation.

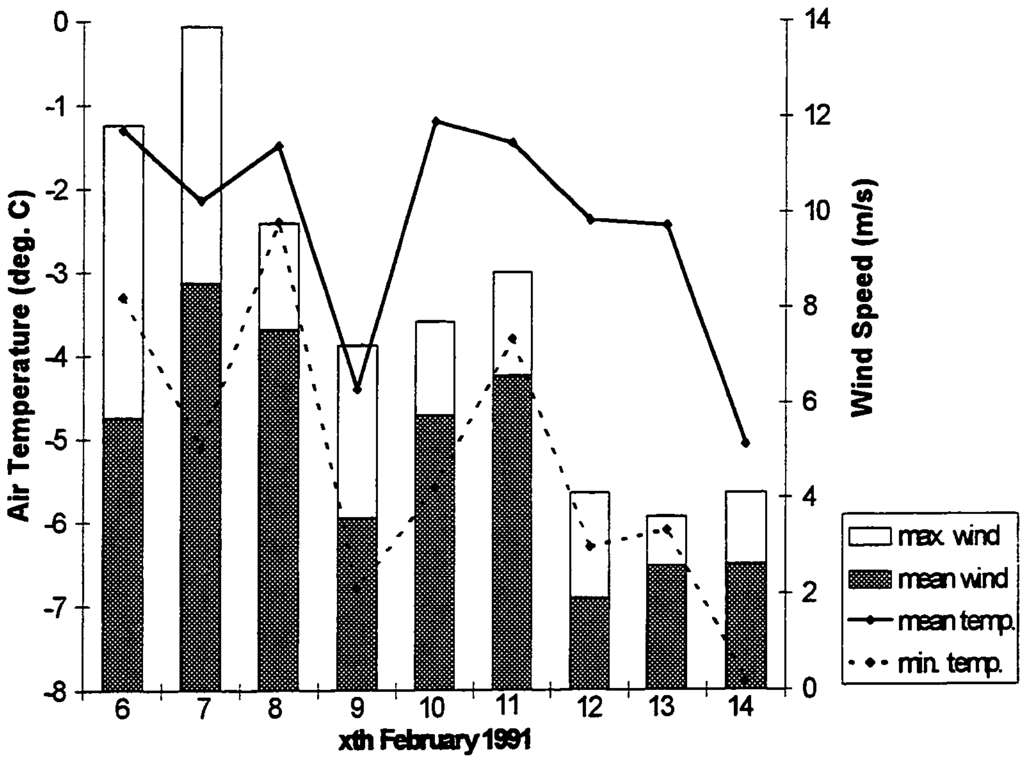
To conclude, during severe weather in February 1991 *robusta* had higher overall energy demands than *britannica*, and was able to survive for shorter periods by the mobilisation of fat and protein reserves. Under conditions where food availability and intake was likely to be significantly reduced, *robusta* needed to assimilate more energy from food than *britannica*. Even though both races were present in the birds which died, I predict that *robusta* were over-represented in those Redshank which died since they were under-insured by body reserves and therefore had a greater reliance on energy assimilated from food when food intake was probably severely restricted. It is unfortunate that the overall racial composition of Redshank that died during periods of severe weather has not been determined

Table 5.5: Mean daily air temperature and windspeed and #energy required from food per day during February 1991 compared to temperature, wind speed and *total daily energy requirement at Teesmouth during February 1983 and 1984 when no large-scale mortality occurred. Percentages in parentheses equal energy required from food as a percentage of daily energy requirements in February 1983 and 1984.

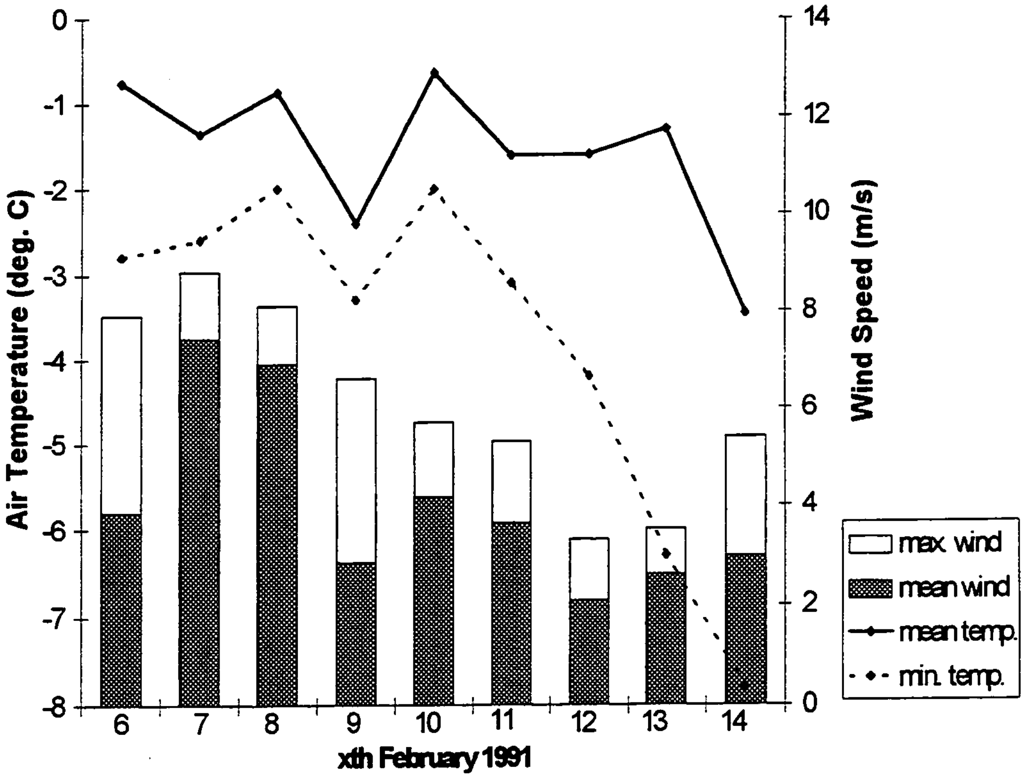
Period	*britannica* mean daily energy requirements KJ/d	*robusta* mean daily energy requirements KJ/d	daily mean air temp. °C	daily mean wind speed m/s
Feb 1983 Teesmouth	311*	379*	2.6	4.3
Feb 1984 Teesmouth	314*	383*	3.8	5.1
6-11 Feb 91 Teesmouth	194# (62%)	264# (69%)	-1.3	4.8
6-14 Feb 91 Teesmouth	238# (76%)	305# (80%)	-1.6	4.0
6-9 Feb 91 The Wash	143# (46%)	221# (58%)	-2.3	6.3
6-11 Feb 91 The Wash	218# (70%)	292# (77%)	-2.0	6.3
6-14 Feb 91 The Wash	255# (82%)	324# (85%)	-2.4	5.0

Figure 5.1: Daily mean and minimum air temperature and daily mean and maximum wind speed at a) The Wash and b) Teesmouth between 6-14th February 1991.

a) The Wash



b) Teesmouth



6.0 General Discussion

6.1 Why do Redshank suffer the highest mortality amongst British wintering shorebirds during severe weather?

A clear distinction between Redshank and other species of shorebirds wintering in Britain is that Redshank exhibit much smaller increases in body mass from autumn to mid-winter. For instance, Grey Plover, Sanderling and Ringed Plover (*Charadrius hiaticula*) over-wintering at Teesmouth increased their body masses by 16%, 17% and 19% respectively above autumn levels (Davidson, 1981; Scott, 1991). In contrast, Redshank at Teesmouth during my study increased body mass by only 8.6% on average, an over-estimate of the increase in individual birds since the proportion of *robusta* increased between autumn and mid-winter. When body mass was controlled for body size, the mid-winter increase in BM was only 5.2%. Both races showed a similarly small mid-winter increase in BM.

However, the shallow peak in body mass did not indicate a similarly low accumulation of fat during mid-winter, since the peak LI s of *robusta* and *britannica* were 18% and 17% respectively. These values compare with LI s of 22% in both Sanderling and Grey Plover at Teesmouth (Scott, 1991), 16% in Dunlin on the Wash (Pienkowski *et al.*, 1979) and 4.7% in Purple Sandpipers from east-coast Britain (Summers *et al.*, 1992). Table 6.1 relates the maximum fat levels of these species to their BMRs to estimate the time over which a species' BMR could be sustained by energy assimilated from fat reserves alone. Grey Plover are better insured than both races of Redshank, in that energy from their fat reserves could sustain BMR for 14days, compared with 10.4 and 11 days for *robusta* and *britannica* respectively. Sanderling, despite their higher LI, are less well insured (i.e. 9.5days) because of a higher mass-specific BMR than Redshank. The low LI of 4.7% of Purple Sandpipers could sustain BMR for only 2 days, representing a very low level of insurance against a negative energy balance during

Table 6.1: Estimated survival time of *britannica, robusta* and four other shorebird species. Survival time equals the number of days over which an energy expenditure equal to BMR could be sustained on mid-winter fat reserves alone.

Species	**Body mass (g)**	**BMR (W)**	**BMR (KJ/d)**	**Lipid Index %**	**Mass of fat (g)**	**Energy (KJ)**	**Survival time (d)**
robusta	151[1]	1.19[1]	102.8	18[1]	27.2	1070	10.4
britannica	144[1]	1.01[1]	87.3	17[1]	24.5	934	11.0
Grey Plover	244[2]	1.75[2]	151.2	22[2]	53.7	2111	14.0
Purple Sandpiper	67[4]	0.70[3]	60.4	4.7[3]	3.2	124	2.0
Dunlin	54[2]	0.58[2]	50.1	16[5]	8.6	338	6.8
Sanderling	53[2]	0.56[2]	48.4	22[2]	11.7	460	9.5

[1] present study; [2] Scott (1991); [3] Summers *et al.* (1992); [4] estimated from shorebird BMR/body mass equation in Scott (1991); [5] Johnson, (1985).

severe winter weather. Since both races of Redshank appear to be relatively well insured in terms of fat reserves (in relation to their BMR) compared to other species, why do Redshank show much higher rates of mortality during severe weather than these same species?

One explanation may be that Redshank are less well insulated than other shorebird species. Table 6.2 compares K_{es} values for *britannica* and *robusta* with those of Turnstone, Grey Plover and Oystercatcher, taken from Kersten & Piersma (1987). The ratios of predicted K_{es} (calculated from the equation of Kendeigh *et al.* (1977) for a non-passerine of the same mass) to actual K_{es}, of both races was no higher than those of the other 3 species (Table 6.2). Therefore, poor insulation is not responsible for the high mortality rate of Redshank.

A more likely explanation is the diet of Redshank and the effect of severe weather on it. To illustrate this argument, consider the Purple Sandpiper, which has the most northerly wintering range of western Palearctic shorebirds, does not show high rates of mortality associated with severe weather, yet, stores little mid-winter fat and consequently, is poorly insured in relation to energy expenditure (Table 6.1). However, Purple Sandpipers may not be poorly insured in relation to the predictability of their food supply and hence the chance of being unable to meet energy demands through feeding (cf. Lima, 1986). Amongst other items, Purple Sandpipers feed on littorinid snails and mussel (*Mytilus edulis*) spat which inhabit rocky intertidal areas and whose availability is less affected by severe weather. Hence, Purple Sandpipers do not need to insure against poor feeding conditions because they are rarely encountered (Summers *et al.*, 1992). Therefore, do Redshank behave according to Lima's (1986) optimisation hypothesis, and store more insurance fat than other species because their food intake is more likely to be reduced in severe weather?

Table 6.2: Comparison of thermal conductivity K_{es} of the two races of Redshank and other shorebird species.

Species	**Mean BM (g)**	**Actual K_{es} (W/°C)**	***Predicted K_{es} (W/°C)**	**Actual K_{es} / Predicted K_{es}**
[1]***robusta***	151	-0.060	-0.042	1.43
[1]***britannica***	144	-0.049	-0.041	1.20
[2]**Turnstone:**				
Individual A	118	-0.048	-0.037	1.30
Individual B	117	-0.053	-0.036	1.47
[2]**Grey Plover:**				
Individual A	169	-0.064	-0.045	1.42
Individual B	258	-0.078	-0.058	1.34
Individual C	286	-0.085	-0.062	1.37
[2]**Oystercatcher:**				
Individual A	540	-0.103	-0.090	1.14

* K_{es} predicted by allometric equation of Kendeigh *et al.* (1977) for non-passerines in winter i.e. $K_{es} = -0.0022 * BM^{0.5886}$

[1] Present study; [2] Kersten & Piersma (1987)

The preferred prey of Redshanks feeding on intertidal mudflats consists mainly of small prey, namely *Corophium* and *Hydrobia* and some larger worms such as *Nereis* (Chapter 4; see also Goss-Custard, Jones & Newbery, 1977; Goss-Custard *et al.*, 1989). In contrast, other large shorebirds such as Grey Plover and Bar-tailed Godwit feed mainly on larger prey consisting of for example, large polychaetes and bivalves (e.g. *Macoma, Scrobicularia*) (e.g. Goss-Custard, Jones & Newbery, 1977; Goss-Custard *et al.*, 1989). Grey Plover and Bar-tailed Godwit therefore require far fewer prey items to achieve the same energy intake rate as Redshank. In fact Pienkowski (1973) found that Redshank wintering at Teesmouth, fed for 90-95% of the tidal cycle, whereas Grey Plover and Bar-tailed Godwit fed for only 60-75% of each cycle. It appears then that the choice of prey by Redshank means that their rate of energy intake is much slower than other species and thus require longer periods of feeding to meet their daily energy requirements. A reduction in the availability of prey during severe weather is more likely to lead to a negative energy balance in Redshank which have less scope to increase their feeding time to achieve the required energy intake, than species such as Grey Plover and Bar-tailed Godwit (with a higher energy intake rate) which have more scope to increase their feeding time.

Why then do Redshank not a) feed on energetically more profitable prey, or b) accumulate more mid-winter fat so that they could survive a negative energy balance for longer periods? Goss-Custard (1977a) argued that despite taking longer to handle large worms, the net energy to be gained by Redshank feeding on them is higher than when taking smaller prey. Appendix IV discusses the possible reasons why Redshank do not feed on more worms, such as a reduction in vigilance whilst feeding, or that the taste of worms is disagreeable to Redshank. Regarding point (b), Redshank are not constrained by food availability in accumulating fat stores between autumn and mid-winter, since captive birds given food *ad libitum* achieved the same mid-winter levels of BM as wild birds at

Teesmouth (Chapter 2). Furthermore, wild Redshank in November were heavier during the 1994/95 winter when densities of prey were lower than in the previous winter when densities were much higher (Chapter 4). The chance of severe weather reducing the availability of prey below a threshold which would allow energy output to be balanced by food intake was therefore greater in 1994/95. Fat storing in Redshank has evolved to set levels in mid-winter controlled in part, by probability of encountering a negative energy balance later in the winter (cf. Lima, 1986).

The reason why these regulated levels are not higher is due to both predation risk and their foraging behaviour. Gosler *et al.* (1995) demonstrated that Great Tits are lighter when predation risk is higher. However as yet, there is no evidence to show a similar effect of predation risk on other species. Redshank certainly experience predation risk which is greater on some estuaries than others. For instance, Cresswell & Whitfield (1994) found raptor predation to have a significant impact on Redshank numbers wintering on the Tyninghame estuary in south-east Scotland. At Teesmouth, from casual observation and carcass searches it appears that although raptors are present throughout the winter, the level of predation on Redshank is much less than at Tyninghame.

Redshank are opportunistic in their feeding behaviour; for example, they often feed away from exposed mudflats, either in tidal creeks, or inland on fields or freshwater habitats. By doing so, they may be able to exploit areas of temporarily greater prey availability, but perhaps more importantly, are able to avoid exposure to high winds which substantially increase heat loss. During very low temperatures which cannot be avoided by behavioural strategies, Redshank may be forced to feed on exposed mudflats since other areas such as fields may be frozen or creeks may be blocked with ice (Pilcher, 1964). Therefore, by having to feed in exposed areas with low prey availability, Redshank quickly reach a negative energy balance which often leads to death. Why then have Redshank not evolved to cope better with these occasional severe periods of low temperatures? Severe conditions which lead to increased mortality in Redshank only occur sporadically, about every 5 years and are usually localised in their effects. The selective effect of severe weather mortality is therefore not constant and is rarely widespread. It appears that the genetic variation in wintering populations of Redshank prior to the large scale mortality events, returns during intervening periods of 'normal' winters. The ability to regenerate genetic variation in Redshank populations is probably aided by the following factors: i) a large proportion of Redshank breed in their first year; ii) Redshank are short-lived (around 5 years) compared to other shorebirds, iii) wintering populations are composed of individuals originating from different breeding populations and thus, the efects of localised severe weather mortality would be diluted on the breeding grounds.

6.2 Is the chance of mortality during severe weather greater in *robusta* than *britannica*?

The evidence from my study suggest that the answer to this question is in fact, "yes". In order to confirm this prediction, future studies of living Redshank on British estuaries during both mild and severe winter weather, and of Redshank which have died during severe periods, should distinguish between the two races. Clark *et al.* (1993) found that the mean wing-length of Redshank which died on the Wash following severe weather in 1991 was longer than that of live Redshank measured in previous 'mild' years, suggesting that *robusta* were over-represented in those birds which died. However, without data on racial proportions of the population before severe weather and of the corpses found afterwards, the differential effect of severe weather on the survival of two races of Redshank can only be surmised and not proven at present. My study predicted that *robusta* had a greater chance of dying in severe weather because i) *robusta* are under-insured i.e. fat reserves make up the same proportion of total body mass as in *britannica,* but would allow a shorter period of survival without food, since ii) *robusta* have a higher rate of energy expenditure resulting from a significantly higher mass-specific BMR and thermal conductivity (i.e. K_{es}).

At high levels of total expenditure, a higher mass-specific BMR would be advantageous since tissues would be metabolising at lower rates (considered as a multiple of BMR) than in animals with the same total energy expenditure but lower mass-specific BMR. Hence, the higher mass-specific BMR of *robusta* could be argued to be an adaptation to higher rates of energy expenditure resulting from either a) breeding at a higher latitude (cf. Weathers, 1979) or b) undergoing long-distance migration between breeding and non-breeding grounds (cf. Kersten & Piersma, 1987). However, any advantage obtained by *robusta* over *britannica* by having a higher mass-specific BMR, appears to have been offset by the higher thermal conductivity of *robusta*. It appeared that the higher thermal conductivity of *robusta* was a result of their larger mass-specific heat production, rather than less well insulated plumage. Further investigation on the thermal properties of the plumage of the two races is required (see Walsberg (1988a) for possible methods).

Despite larger energy demands, there appeared to be no difference in foraging behaviour between the two races, in terms of either foraging duration or diet choice. The resolution of the protocol used may, not however, have been sufficient to identify differences associated with race when there was clearly a large amount of variation in foraging behaviour between individuals.

My study has shown significant differences in the ecophysiology of two races of the same species wintering in the same area which have significant implications for the survival and ecology of the two races. This study therefore highlights the need for studies of other shorebird species to concentrate not only on a species level, but to consider the possible influences of differences lifestyles and breeding or wintering origins of different populations which are present within the same study area.

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APPENDIX I

Examination of the use of discriminant function analysis to distinguish between races of Redshank

Introduction

In order to test the robustness of the discriminant function of Summers *et al.* (1988) and its applicability to my study, biometric data taken from Redshank ringed and then recaptured at Teesmouth (1983-1995) were examined to determine the degree of variation in measurements between workers and its effect on racial identification. The possibility of sexual bias in the birds which could be classified or not classified by the discriminant function was investigated in a sample of Redshank of known sex which died following severe weather on the Wash in 1991.

Discriminant function analysis has been used widely for the identification of sex in birds which show no sexual dimorphism in plumage or appearance, but differ in size (e.g. Fox *et al.*, 1981; Granadeiro, 1993; Hamer & Furness, 1991; Soloviev & Tomkovich, 1995). In these studies the discriminant function determined identity on a binomial basis, i.e. a bird was either male or female. However, mis-classification can arise due to variability amongst workers taking the measurements which are used in the discriminant function (Hamer & Furness, 1991). Some studies (Green, 1982; Maron & Myers, 1984; Wood, 1987) applied probabilities to obtaining a particular discriminant score for a female or male bird. Likewise, the discriminant function derived by Summers *et al.* (1988) and used in my study, assigns a probability to its prediction i.e. a bird has a 0.0-1.0 probability of being of Icelandic origin (*robusta*). Therefore, it is possible to create an error margin for the predictions; for example, in my study only those birds with a probability of 0.7-1.0 of being Icelandic (*robusta*) were classified as Icelandic, whilst those with probabilities of 0.0-0.3 were classified as British (*britannica*); birds with probabilities of 0.4-0.6 were not assigned to a particular race. It was hoped that these strict criteria were sufficient to prevent birds being assigned to the wrong race as a result of variation between measurers.

The Icelandic race *robusta* is larger in overall body size than *britannica* and hence, the former has significantly longer wings and tarsus-toe, but has a shorter bill (Hale, 1971; Summers *et al.*, 1988). In addition, within each race, females are larger than males (Hale, 1971) which creates a good deal of overlap in the size of biometrics of the two races. It could therefore be argued that the discriminant function (with a probability threshold of 0.7) can only classify those individuals at either end of a size cline; i.e. the majority of Redshank classified as *britannica* may be the smaller males, whilst the majority of birds classified as *robusta* may be the larger females.

Methods

Effect of variability in measurements

Biometric data were examined from 1,470 captures and recaptures of adult Redshank ringed at Teesmouth between 1983 and 1995. Wing-length (maximum chord) and tarsus-toe were measured to the nearest 1mm using a stopped rule; bill-length was measured to the nearest 0.1mm using vernier callipers. Differences in wing-length, bill-length and tarsus-toe length of individuals between capture and recapture were calculated. The identity of the measurer was assigned only to a group of ringers (i.e. Durham University or Tees R. G.) until August 1992 when from then on, individual measurers were identified. Paired t-tests were performed on biometrics taken from the same bird but by different workers (it was assumed that a different person had taken the measurements unless specified). From 1992 onwards, most measurements were taken by one individual (R. M. Ward). Paired t-tests were performed to determine the extent of variation between measurements taken by RMW alone and to determine the extent of any bias in measurements when compared to those taken by other workers. All wing-lengths were corrected for seasonal wear (Summers *et al.*, 1988) and no wing-lengths were used which had been taken from birds which were moulting their outer 2 primaries. It was assumed that no natural seasonal variation existed in lengths of bill and tarsus-toe since all the birds used in these analyses were fully grown adults.

Where all 3 biometrics had been taken, the birds were assigned a probability of being Icelandic (0-1) using the discriminant function of Summers *et al.* (1988) and assigned to a race accordingly (see above).

Sexual bias

Male and female Redshank do not exhibit any external morphological differences which could be used to distinguish them and hence sex can be determined only by the dissection of dead birds. A sample of Redshank corpses taken from The Wash, south-east England following severe weather in February 1991 (supplied by N. A. & J. A. Clark, British Trust for Ornithology, Thetford) provided the rare opportunity of being able to investigate the presence of sexual bias in the discriminant function.

Measurements of wing-length, bill-length and tarsus-toe were taken using the same techniques as above on 121 corpses of adult Redshank. Each measurement was taken by the same person (P. L. Ireland: wing-length and tarsus-toe; S. Entwhistle-Baker: bill-length). Racial origin was predicted using the discriminant function of Summers *et al.* (1988) Sex was determined by dissection.

Results

Effect of variability of measurements

The mean differences in the three biometrics between different measurers are given in Table 1. Overall, differences between measurers were significant for all three biometrics (Table 1). This was also true for repeated measurements made by the same person (Table 2). In both cases, the greatest mean difference was in wing-length. However, when the absolute differences are expressed as a percentage of the population median for the particular measurement, bill-length shows the greatest difference both between and within measurers (Table 1 & 2). The mean absolute difference between repeated measurements was less when a single measurer was involved than if different people took the measurements (Tables 1 & 2); however, only tarsus-toe measurements showed a significant reduction (T-test $t_{106}=19.52$, $P<0.001$).

Overall, measurements made by RMW of wing-length and bill-length were significantly greater than those taken by other people (Table 3). Failure to straighten the wing completely when attempting to measure the maximum length is a common feature amongst bird-ringers.

This variation amongst and within measurers resulted in only 3 (7%) out of 46 birds changing racial identity between capture and recapture. 12 (26%) birds were either originally assigned to a race and then, as a result of variation in measurements, were unable to be assigned to a race (i.e. $0.3<P<0.7$), or vice-versa. The remaining 31 (67%) birds retained their original racial identity when recaptured.

Sexual Bias

Table 4 shows that in the sample of corpses taken from the Wash, for both *robusta* and *britannica*, females had significantly longer wings than males; though both sexes had similar bill-lengths and tarsus-toe measurements.

There was no significant association between sex and the racial group in which birds were classified i.e. *britannica, robusta* or unknown ($\chi^2_2 = 1.285$, $P>0.05$; Table 5). Therefore, the sex ratio in each racial group did not deviate significantly from that of the whole sample in which males predominated 1.3 : 1.

Table 1. Mean difference (mm) in measurement of bill-length, wing-length and tarsus-toe in adult Redshank made by two different measurers (the sign of the difference was ignored). The percentage in brackets is the mean difference as a percentage of the population median (wing-length=171mm, bill-length=41mm, tarsus-toe=85).

	Wing-length	Bill-length	Tarsus-toe
mean (mm)	2.1(1.2%)	1.03(2.5%)	1.0(1.2%)
s.d.	1.53	0.86	1.11
n	92	123	53
T	11.34	13.29	6.83
P - level	<0.001	<0.001	<0.001

Table 2. Mean difference (mm) in measurement of bill-length, wing-length and tarsus-toe in adult Redshank made twice by the same measurer (RMW) (the sign of the difference was ignored). The percentage in brackets is the mean difference as a percentage of the population median (wing-length=171mm, bill-length=41mm, tarsus-toe=85).

	Wing-length	Bill-length	Tarsus-toe
mean	1.8(1.1%)	0.86(2.1%)	0.6(0.7%)
s.d.	1.29	0.74	0.67
n	16	14	26
T	5.426	4.348	4.680
P - level	<0.001	<0.001	<0.001

Table 3. Mean difference (mm) in measurement of bill-length, wing-length and tarsus-toe in adult Redshank between RMW and other measurers (the sign of the difference was retained).

	Wing-length	Bill-length	Tarsus-toe
mean	1.1	0.58	0.2
s.d.	2.51	1.17	1.45
n	31	52	30
T	2.503	3.57	0.866
P - level	<0.05	<0.001	>0.05

Table 4: Comparison of wing-length, bill-length and tarsus -toe between male and female a) *robusta* and b) *britannica* from a sample of corpses from The Wash in 1991. Values given are means with standard errors in parentheses.

a) ***robusta***

	male (n=28)	**female (n=31)**	**t_{df}**
wing-length (mm)	175.2 (0.54)	178.0 (0.60)	**3.39_{57} ****
bill-length (mm)	41.1 (0.32)	41.4 (0.26)	0.90_{57} ns
tarsus-toe (mm)	86.9 (0.56)	86.3 (0.35)	0.88_{57} ns

b) ***britannica***

	male (n=27)	**female (n=13)**	**t_{df}**
wing-length (mm)	166.6 (0.80)	169.3 (0.55)	**2.77_{38} ***
bill-length (mm)	42.4 (0.28)	42.7 (0.39)	0.55_{38} ns
tarsus-toe (mm)	82.7 (0.48)	83.5 (0.56)	0.56_{38} ns

ns not significant * significant with a probability level of P<0.05

** significant with a probability level of P<0.01

Table 5: Chi-square contingency table of sex and racial origin of Redshank corpses from The Wash in February 1991 ($\chi^2_2 = 3.55$, $P>0.05$) Value in parentheses equals $(O - E)^2 / E$

	male	**female**	
robusta	O=28 E=33 (0.76)	O=31 E=26 (0.96)	**59**
britannica	0=27 E=23 (0.70)	O=13 E=17 (0.94)	**40**
unknown	0=13 E=12 (0.08)	O=8 E=9 (0.11)	**21**
	68	**52**	**120**

Discussion

Effect of variability in measurements

This study, like other studies (eg. Barret *et al.*, 1989) shows that measurements of body structures in birds are not precisely repeatable. This results in the observed variation between measurers and also when measurements are repeated by the same person. Bill length appears to be the most variable and does not come close to the precision of 0.1mm at which it should be measured using vernier calipers. Tarsus-toe length appears to be the most repeatable in that the mean absolute error between measurers is only 1mm, which could be attributed to the precision with which this measurement is taken (normally 1mm). Furthermore, tarsus-toe length exhibited no bias attributable to the individual measurer used in this study.

Although significant, the variation in measurements between measurers was small in absolute terms and had surprisingly little effect on the prediction of racial identity. It appears that the range of probabilities chosen for this study over which no race is assigned is a sufficient buffer to prevent variation in measurements mis-classifying the race of a Redshank. Since in my study, mean physiological parameters of the two races are being compared, the potential errors resulting from mis-classification of one or two indiviuals are minimal.

In general, when using discriminate functions to identify race, sex, age etc., errors in classification resulting from lack of repeatability in measurements can be reduced by using measurements taken by as few observers as possible or ideally by the person whose measurements were used to formulate the discriminant function (Hamer & Furness, 1991).

Sexual Bias

If the discrimant function was classifying individuals based purely on size then those predicted to be *robusta* would contain proportionally more females compared to the sample as a whole which was not the case. Likewise, males were not over-represented in the group predicted to be *britannica.* It appears then that the discriminant function was discriminating on shape (i.e. the size of each measurement in relation to each other) rather than overall body size alone.

APPENDIX II

Validation of the use of Total Body Electrical Conductivity (TOBEC) for estimating total lean mass and mass of fat in live Redshank

Introduction

In this study I develop and test existing predictive formulae of Scott *et al.* (1991) and Scott *et al.* (1994) utilising TOBEC to estimate total lean mass (TLM) and hence, lipid mass (FM) in Redshank.

Previous studies of nutrient stores and reserves in shorebirds (e.g. Evans & Smith 1975, Davidson, 1981a, 1982a) have obtained measures of lean mass and fat levels using solvent extraction of lipids. Destructive methods of nutritional analysis of birds have major limitations. They are expensive and time consuming and both legislative and logistical restrictions associated with taking birds from the wild result in small sample sizes (Blem, 1990). In addition, ethical questions arise when killing samples of birds which eventually produce small sample sizes and often inconclusive results. The use of non-destructive methods of analysis alleviate most of these restrictions and have the added advantage of being able to follow the changes in nutritional condition of individuals through time.

Techniques for the non-destructive analysis of nutrient reserves in birds can be divided into those which measure mass of fat and those which measure the total lean mass. The traditional and most widely used method to measure mass of fat in birds is "fat-scoring" of visible subcutaneous deposits (e.g. Helms & Drury, 1960; Kaiser, 1993). Whilst fat scoring can give meaningful estimates of average fat-loading in groups or populations, its precision is not adequate to monitor fat-level changes in individuals (Scott *et al.*, 1995). Formulae based on several skeletal measurements (e.g. wing-length, bill-length) have been used to predict the total lean mass (TLM) of shorebirds (e.g.Davidson, 1983) and hence, by deduction from body mass, mass of fat. However, these formulae take into account variation in TLM attributable only to body size and not that which can occur within a single individual due to season. Castro & Myers (1990) found that the application of formulae predicting mass of fat in Sanderling *Calidris alba* from body mass and external morphology had to be restricted to the population from which the formulae were derived. They found that for a particular body size TLM differed between populations from different locations. Even if such formulae are restricted to specific date periods and to single populations (Davidson, 1983) they are still ineffective if TLM deviates from 'normal' levels due to stochastic events such as severe weather (e.g. Beecroft & Clark, 1986).

Another method of estimating TLM in a live bird is from its Total Body Electrical Conductivity (TOBEC). TOBEC is highly correlated with TLM (Walsberg, 1988; Castro *et al.*, 1990; Roby, 1991; Scott*et al.*, 1991; Skagen *et al.*, 1993) and has been shown to be a reliable predictor of TLM (Roby, 1991; Scott *et al.*, 1991; Skagen *et al.*, 1993). The relationship between TOBEC measurements and actual TLM must be determined by sacrificing a small sample of individuals of a given species immediately after measurement of their TOBECs and later obtaining their TLM by destructive analysis. Predictive models derived from single species give more accurate estimates of TLM than those obtained from inter-specific models (Scott *et al.*, 1991). The methods employed by different studies for calibrating TOBEC have been highly variable and will be discussed later.

By subtracting from total body mass the TLM estimated from the TOBEC index, a predicted total lipid mass PFM can be estimated (Castro *et al.*, 1990; Roby, 1991; Scott *et al.*, 1991; Scott *et al.*, 1994, 1995). The same absolute error is attached to PFM as to the predicted total lean mass PTLM, but it usually represents a greater proportion of the actual lipid mass since TLM usually exceeds fat mass (Morton *et al.*, 1991). The most recent studies (Skagen *et al.*, 1993; Conway *et al.*, 1994; Meijer *et al.*, 1994) employing TOBEC to estimate lipid mass have predicted lipid mass directly from multiple regressions with TOBEC as an independent variable alongside body size measures.

Methods

In order to obtain estimates of TLM from TOBEC, measurements of TLM obtained from carcass analysis must be regressed against TOBEC indices to produce a predictive model. Scott *et al.* (1991) demonstrated that intraspecific models are better predictors than interspecific ones. It was intended to add to and test the model of Scott *et al.* (1994) based on 6 wild and 2 captive Redshank. The methods of carcass analysis outlined below closely follow those used by Scott *et al.* (1991, 1994).

The TOBEC indices of 7 Redshank which had been held in captivity for between 2 and 3 months were measured (see section 2.2.4) immediately before they were killed by cervical dislocation. Three birds were weighed, sealed in polythene bags and frozen, whilst the remaining five were dissected immediately after death. The body cavity was opened from the furcular region to the pelvic girdle to aid drying. The left pectoral muscle block (pectoralis major and supracoracoideus), liver, stomach and intestine were dissected out after as much subcutaneous lipid as possible had been removed. The organs and dissected carcass were weighed to the nearest mg on a torsion balance. The masses of each organ and the carcass were added together to obtain total body mass (BM). The purpose of the dissection (which was not performed by Scott *et al.* 1991, 1994) was to compare organ masses of captive birds with those of wild birds (see chapter 2). The carcass and organs were dried to constant mass in a vacuum oven at 40°C and added together to give total dry body mass (TDBM). Once dry, the organs were placed back inside the body cavity and lipid was extracted from the whole carcass using Sohxlet apparatus and chloroform as a solvent. After all lipid had been extracted, the carcasses were dried to constant mass to give the total lean dry mass (TLDM). TLDM was subtracted from TDBM to give the mass of lipid (FM). FM was subtracted from BM to give total lean mass (TLM). A summary of measurements and their abbreviations is given in Table 1. The three corpses which were frozen immediately after death, were defrosted later, the body cavity opened from the furcular region to the pelvic girdle (no organs were removed) and then analysed as above.

Linear regression and second order polynomial models were fitted to plots of TLM and TOBEC index (I), the independent variable, to give estimates of total lean mass, $PTLM_1$ and $PTLM_2$ respectively. The strength of these models in predicting total lean mass from TOBEC measurements was tested using cross-validation (Skagen *et al.*, 1993). This technique involved removing an individual from the predictive model, estimating the lean mass of the same individual using the new models, and then comparing $PTLM_1$ and $PTLM_2$ with the actual TLM. The procedure was then repeated for each individual used in the calibration. $PTLM_1$ and $PTLM_2$ were deducted from BM to derive the estimates of lipid mass, PFM_1 and PFM_2. In order to produce an estimate of lipid mass PFM_3 with an error independent of that associated with predicting TLM, a multiple regression was

Table 1: Definitions and abbreviations of terms of body composition

Abbreviation	Definition
BM	Total body mass
TOBEC	Total body electrical conductivity
I	Index of TOBEC produced by EM-Scan SA1 Small Body Composition Analyser
TLM	Total lean or fat-free mass
PTLM$_1$	Total lean mass predicted by the linear regression of TLM with I (equation 1)
PTLM$_2$	Total lean mass predicted by the second order polynomial of TLM with I (equation 2)
FM	Lipid mass = BM - TLM
PFM$_1$	= BM - PTLM$_1$
PFM$_2$	= BM - PTLM$_2$
PFM$_3$	Lipid mass predicted by the multiple regresssion of BM and TOBEC (equation 2.3)

used with FM as the dependant variable and BM and TOBEC index (I) as independent variables (Morton *et al.* 1991) by forced entry (James & McCulloch, 1990). Cross-validation was used to calculate the error associated with PFM_3.

Results

One bird from the sample taken from Scott *et al.* (1991) had a significant leverage on regression equations of I and TLM and was thus removed from the data used to formulate calibration equations for TOBEC (Skagen *et al.*, 1993).

The linear (Figure 1) and second-order polynomial models generated to predict TLM from I are shown below in equations 1 and 2 respectively.

$$PTLM_1 = 0.288 * I + 55.5 \qquad r^2 = 0.87 \qquad 1$$

$$PTLM_2 = 0.207 * I - 0.00018 * I^2 + 64.2 \quad r^2 = 0.87 \qquad 2$$

Multiple regression of independant variables BM and I yielded the following predictive model for lipid mass PFM_3:

$$PFM_3 = 0.947 * BM - 0.276 * I - 50.7 \quad r^2 = 0.88 \quad 3$$

Cross-validation yielded mean errors of 4.3g for $PTLM_1$ and 4.7g for $PTLM_2$, representing 3.5%, 3.8% of actual TLM respectively; and likewise, 4.3g for PFM_1 and 4.7g for PFM_2, and 4.9g for PFM_3, representing 23.6%, 25.7% and 24.8% of actual FM respectively (Table 2). The absolute error of estimation was not proportional to the actual TLM or PFM being predicted (Figure 2). Since mean errors were lowest for $PTLM_1$ and PFM_1, they were used as estimates of TLM and FM in Chapter 2 and were referred to as PTLM and PFM respectively.

Figure 1: Relationship between total lean mass (TLM) and TOBEC index.

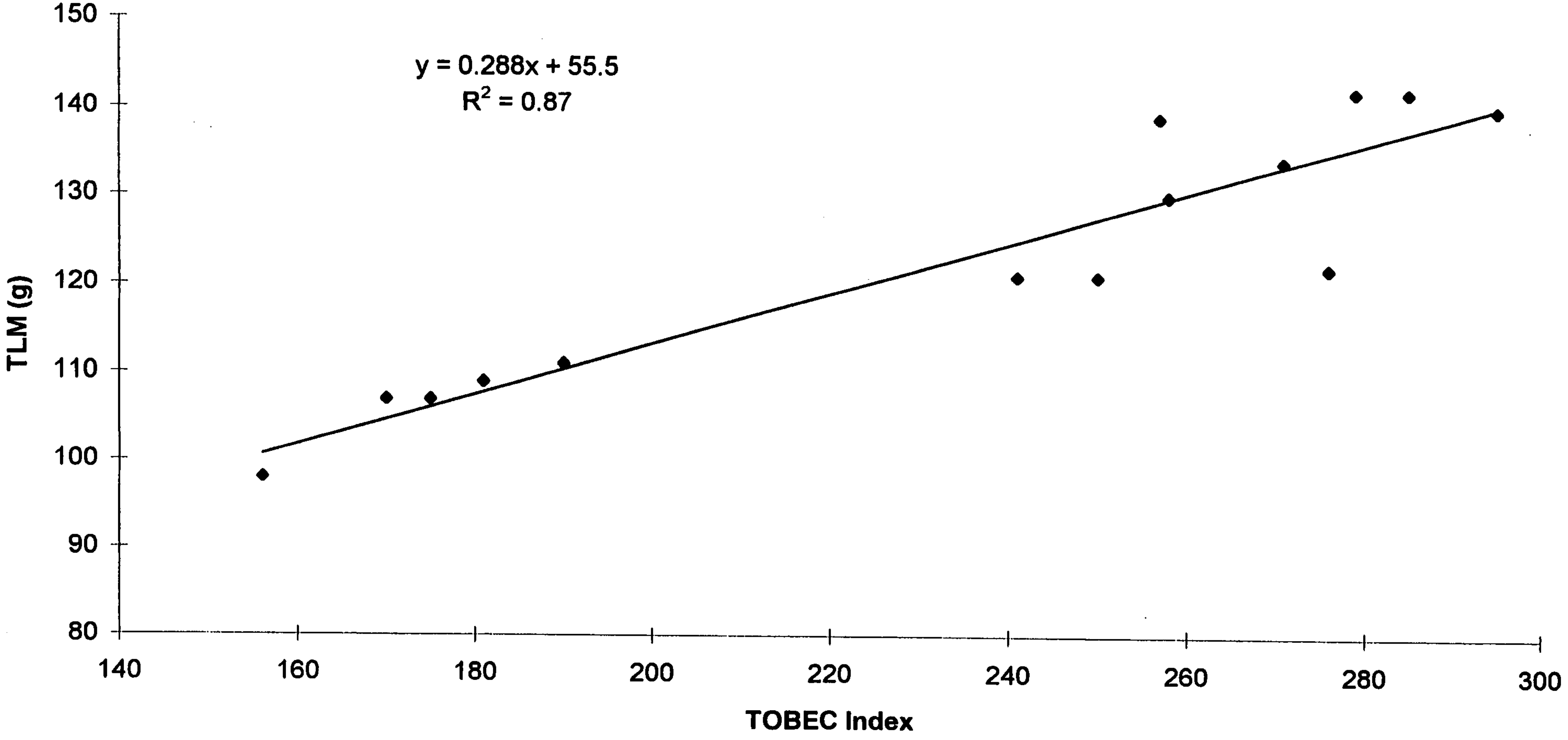


Table 2: **Cross-validation comparison of measurements of total lean mass and lipid mass obtained from destructive analysis (TLM, FM) and using predictive models derived from Total body electrical conductivity TOBEC (PTLM, PFM).**

ID	BM g	% water	TLM g	PTLM 1 g	PTLM 2 g	TLM - PTLM$_1$	TLM - PTLM 2	FM g	PFM$_1$ g	PFM$_2$ g	PFM$_3$ g	FM - PFM$_1$	FM - PFM$_2$	FM - PFM$_3$
*1	157	68.4	142.0	135.0	135.0	7.0	7.0	14.9	22.0	22.0	22.0	7.0	7.0	7.0
*3	146	64.7	133.9	133.4	133.5	0.5	0.4	12.2	12.6	12.6	13.0	0.5	0.4	0.8
*4	152	66.1	140.4	140.4	141.1	0.0	0.7	11.6	11.6	10.9	11.9	0.0	0.7	0.4
*5	160	66.3	142.1	136.6	136.4	5.5	5.7	17.9	23.4	23.6	23.2	5.5	5.7	5.3
*6	156	67.1	139.5	128.6	127.6	11.0	11.9	16.5	27.4	28.4	27.1	11.0	11.9	10.6
*W	194	63.0	129.6	129.8	128.9	0.2	0.7	64.4	68.2	69.1	67.1	0.2	0.7	1.3
*GW	131	63.0	106.8	105.5	105.8	1.3	1.0	24.2	25.5	25.2	25.2	1.3	1.0	1.0
LLW	130	65.4	106.7	103.8	104.0	3.0	2.7	23.1	26.1	25.8	25.9	3.0	2.7	2.8
LLR	179	66.1	120.8	128.0	128.4	7.2	7.6	58.2	51.0	50.6	47.2	7.2	7.6	11.0
LLY	136	66.5	122.3	136.9	137.2	14.5	14.9	13.9	-0.66	-1.02	-2.6	14.5	14.9	16.5
LLG	172	66.8	121.4	125.3	125.6	3.9	4.2	50.2	46.2	46.0	44.2	3.9	4.2	6.0
YT	115	62.7	97.6	101.5	104.0	3.9	6.3	17.0	13.1	10.7	13.8	3.9	6.3	3.2
LWR	131	65.8	109.0	107.4	107.6	1.6	1.5	22.1	23.7	23.6	23.7	1.6	1.5	1.5
LWG	139	66.5	110.9	110.1	109.9	0.8	1.0	27.6	28.7	28.7	28.2	0.8	1.0	0.7
Mean	149.9	65.6	123.1	123.0	123.2	±4.3	±4.7	26.7	27.05	26.9	26.4	±4.3	±4.7	±4.9
s.d.	21.7	1.7	15.2	14.1	13.8	4.4	4.5	17.6	17.8	18.1	17.2	4.4	4.5	4.9

* Analyses carried out by I. Scott (see Scott *et al.*, 1991 & 1994)

$PTLM_1$ = aTOBEC + c $PTLM_2$ = aTOBEC +b(TOBEC)^2 + c

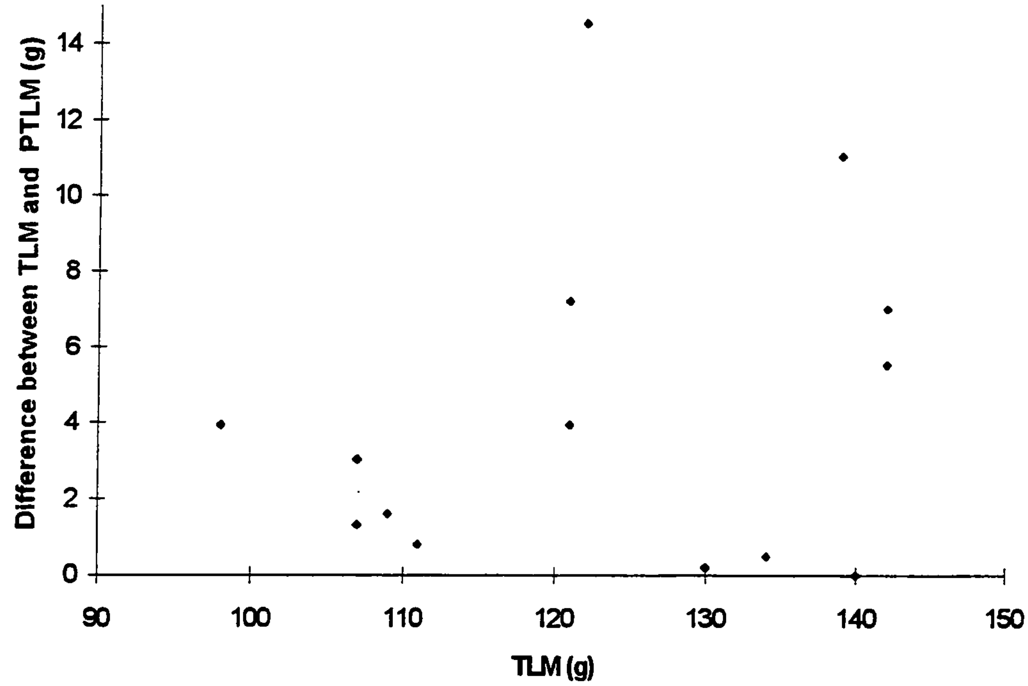
PFM_1 = BM - $PTLM_1$ PFM_2 = BM - $PTLM_2$

PFM_3 = aBM - bTOBEC + c

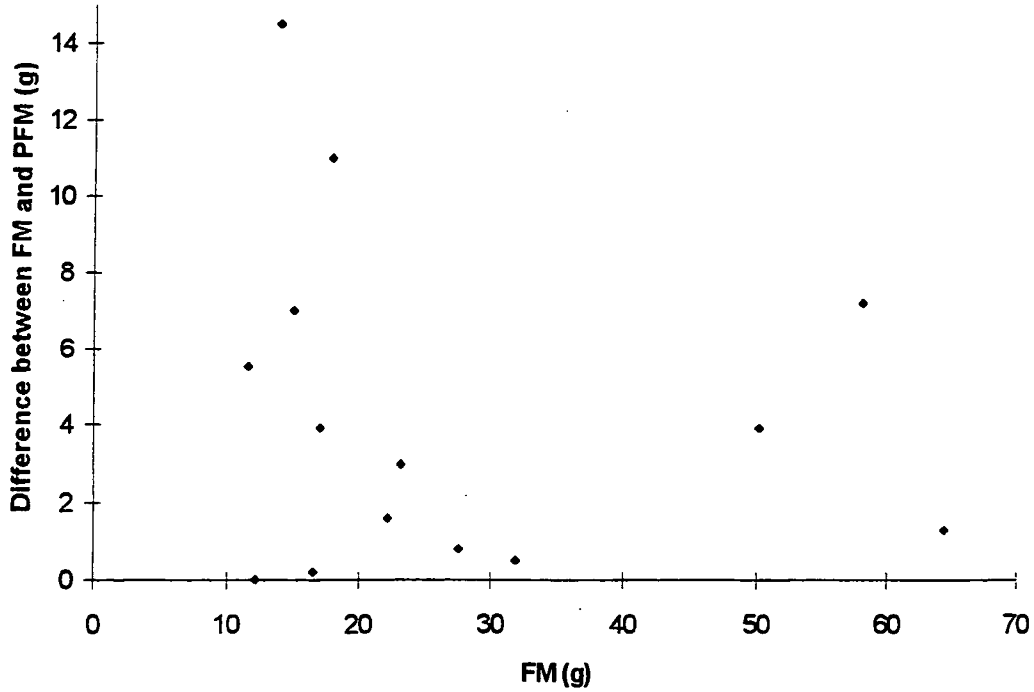
See Table 2.1 for key to abbreviations

Figure 2: The error of predicting a) total lean mass (i.e. difference between TLM and PTLM$_1$) and b) lipid mass (i.e. difference between PFM$_1$ and FM) compared to the actual quantity of TLM and FM being estimated.

a) TLM: correlation coefficient $r_{12} = 0.213$, $P>0.05$



b) FM: $r_{12} = -0.169$, $P>0.05$



Discussion

Calibration and validation of TOBEC for estimating total lean mass

The smallest range and mean of error in estimating PTLM was achieved using a linear regression of TLM and TOBEC with the latter as the dependent variable. Before the removal of one of the data points taken from Scott *et al.* (1991) the relationship between TLM and TOBEC was a second order polynomial, the curvature of which was created by this single data point which had a TOBEC of 440 and a TLM of 149g. The resultant polynomial model appeared unrealistic since it reached an asymptote at 150g and PTLM started to decline at I=460. A Redshank with a TLM of 150g certainly does not represent the upper size limit for which the SA-1 can operate, since Roby (1991) found a significant positive relationship to exist between I and TLM in Northern Bobwhites (*Colinus virginianus*) which had a lean mass ranging from 160-260g. Whilst the interspecific relationship betwen TLM and I is curvilinear (Walsberg, 1988; Scott *et al.*, 1991), intraspecifically, the relationship between TLM and I is better explained by a linear relationship (Scott *et al.*,1991; Roby, 1991; Meijer *et al*, 1994). Table 3 shows how the slopes of linear models of TLM and I are steeper in species with lower TLMs. Since the relationship between TLM and I does not appear to level off within a species at high values of TLM, the difference in slopes between species is probably a result of differences in body shape as well as size. Removing the anomalous Redshank data point was therefore valid, since incorporating it produced an unrealistic model in light of the known relationships between TLM and I in other species of bird of both smaller and larger TLM than Redshank. The high value of I of the point removed may have been due to the bird having wet plumage, or a high body temperature resulting from capture stress, or moving excessively in the chamber (Scott *et al.,* 1991).

Table 3: **Equations predicting total lean mass TLM from TOBEC index I in different species and different studies.**

Species	Study	TLM range (g)	predictive equation	r^2	n
Calidris pusilla	Skagen *et al.*(1993)	19.7 - 24.4	*TLM=0.60I + 10.25	0.79	20
Calidris fuscicollis	Skagen *et al.*(1993)	33.4 - 40.7	*TLM=0.39I + 18.33	0.68	21
Calidris alpina	Scott *et al.* (1991)	28 - 50	TLM=0.53I + 21.4	0.71	11
Charadrius hiaticula	Scott *et al.* (1991)	50-67	TLM=0.36I + 33.7	0.93	6
Sternus vulgaris	Scott *et al.* (1991)	66-86	TLM=0.30I + 45.6	0.96	10
Sternus vulgaris	Meijer *et al.* (1994)	61.0 - 77.7	TLM=0.32I + 39.5	0.56	18
Tringa totanus	This study	97.6 - 142.1	TLM=0..29I + 55.5	0.87	14
Colinus virginianus	Roby *et al.* (1991)	161 - 255	*TLM=0.17I + 73.1	0.99	62

* equation originally derived with TLM as independant variable and I as dependant variable.

It is difficult to compare the accuracy of the model in this study with that of others, since the methods used to test the accuracy of predictive models of TLM and TOBEC in other studies is highly variable. Scott *et al.* (1991) predicted TLM in five Starlings from a linear model derived from 15 other individuals with a mean error of 0.9g over a range of TLM of 65-85g. This truly independent form of testing of predictive models should be the ideal method of determining errors associated with the prediction. Quoting r^2 values or using inverse regression procedures to attach confidence intervals to predictive models (Castro *et al.*, 1990; Roby, 1991; Kaiser, 1993; Meijer *et al.*, 1994) does not actually test the predictive accuracy of the models (Morton, 1991; Skagen *et al.*, 1993) but merely describes how closely the data used to create the model fit the model (Perdeck, 1985). However, using an independent sample to test the accuracy of the model requires the sacrifice of even more birds. This may not always be possible due to logistical, legislative or ethical constraints. The cross-validation technique used in this and other studies (Skagen *et al.*, 1993; Conway *et al.*, 1994) incorporates a degree of independence into the test without increasing the number of birds sacrificed.

Skagen *et al.* (1993) used cross-validation to test the estimation of PTLM by intra-specific models of TLM and TOBEC (dependent variable) of Semi-palmated Sandpipers (TLM of 20-24g) and White-rumped Sandpipers (*Calidris fuscicollis*) (TLM of 31-40g) and found mean errors to be 3.3% ± 0.42%(SE) and 3.5% ± 0.52%(SE) respectively of the TLM being estimated. Expressing errors as percentages of the quantity being estimated is often used to quantify the relativity of error of prediction (Morton *et al.*, 1991; Scott *et al.*, 1991; Skagen *et al.*, 1993; Conway *et al.*, 1994). However, the usefulness of expressing errors as percentage is questionable and potentially misleading. A mean absolute error in estimating TLM of for example 5g would equate to a 10% error in a bird of 50g, but only a 5% error in a 100g bird. This would suggest that in larger birds the error of prediction is smaller, which is misleading since the absolute error was the same. In my study the absolute error of prediction did not correlate with the quantity being predicted (Figure 2). Errors are more indicative of the accuracy of the application of a predictive model if they are expressed in absolute terms and in the context of the range over which parameters such as TLM are being estimated. If the error exceeds the range over which TLM will change either between individuals or within individuals (depending on the comparisons being made), then the resolution of the model obviously is not fine enough.

Skagen *et al.* (1993) obtained mean absolute errors in estimating TLM of 0.71g ± 0.826g(95% CI) in Semi-palmated Sandpipers (TLM of 20-24g) and 1.32g ± 1.939g in White-rumped Sandpipers (TLM of 31-40g), which expressed as percentages of the range of TLM being predicted (4g and 9g respectively) equates to 18% ± 20% and 15% ± 21.5%. The resolution of the model used in my study to estimate TLM over a range of TLM of 97-142g was 9.6% ± 5.6%(95% CI) (absolute mean error 4.31g ± 2.51g). The resolution of this model was sufficient for the purposes for which I used it. For example , the mean reduction in PTLM within individual Redshank after being brought into captivity was 16.9g which far exceeds any error which would have been attributable to the resolution of the predictive model. The potential effect of prediction errors on estimation of changes in TLM (and FM and LI) in individuals was reduced in my study by comparing the within-individual changes of groups of individuals using paired parametric or non-parametric t-tests. Likewise, the effect of error on determination of seasonal changes in TLM (and FM and LI) was reduced by comparing the means of groups of individuals at different times. In future studies, the use of TOBEC should be evaluated in the context of the questions which it is being used to answer.

During the formulation of models of PTLM in this study, TLM was quoted as the dependant variable and TOBEC as the independent in accordance with Walsberg

(1988) and Scott *et al.* (1991, 1994). Conversely, other studies (e.g. Castro *et al.*, 1990; Roby, 1991; Meijer *et al.*, 1994; Skagen *et al.*, 1993) assumed the error in measuring TOBEC to be greater than that in determining TLM from destructive analysis and had therefore used TLM as the independant variable However, I have found measurements of TOBEC using the SA-1 to be highly repeatable, both within and between observers, and nothing in the literature contradicts these observations. Therefore, since error arising from measurement of TOBEC is negligible (in dry birds of normal hydration and not wearing British or European metal rings) and TLM is to be the variable predicted, TLM should be used as the dependant variable in regressions with TOBEC (Zar, 1984).

The errors arising from different approaches to destructive analysis of carcasses are highlighted by Skagen *et al.* (1993) who tested predictive equations of TLM and TOBEC derived by Castro *et al.* (1990)(based on 8 species including those used by Skagen *et al.*) and Scott *et al.* (1991) (based on Dunlin of similar TLM to those used by Skagen *et al.)* on Semi-palmated Sandpipers and White-rumped Sandpipers. Errors incurred were high, which was partly due to the different ways in which fat was extracted. Scott *et al.* (1991) used chloroform whilst Skagen *et al.* (1993) and subsequent studies have used petroleum ether; Castro *et al.* (1990) used a mixture of the two. Pet. ether extracts only triglycerides (storage lipids) whilst chloroform removes all lipids including phospholipids (structural lipids) as well as some non-lipid compounds (Dobush *et al.*, 1985; Blem, 1991). Hence both solvents have their drawbacks when used for calibrating with TOBEC indices, since TOBEC is affected only by lean mass which will be over-estimated by petroleum ether extraction but under-estimated by chloroform extraction. If carcass analysis is being used to test the predictive accuracy of models derived from other studies, it is important that the extraction technique is the same as that used to create the predictive model. Another source of error in estimating TLM by destructive analysis is the temperature at which the carcasses are dried. This is generally 60-70°C in normal oven, which could be considered too high since more volatile lipids will evaporate creating an overestimate of TLM (Blem, 1991). In the absence of freeze-drying, which is not ideal because it does not remove all water, carcasses in my study and in Scott *et al.* (1991) were vacuum-dried at 40°C, which prevents evaporation of lipids.

Meijer *et al.* (1994) compared their model relating TOBEC to TLM for Starlings with the intra-specific model of Scott *et al.* (1991) and despite sample sizes being similar (n=14 and 15 respectively), found $r^2 = 0.56$ for the Meijer model whereas $r^2 = 0.96$ for the Scott model. This difference in strength of the relationship between TLM and TOBEC could have resulted from the methodological differences in carcass analysis described above. Additionally, TOBEC was measured by Meijer *et al.* (1994) on birds which were anaesthetised. This was probably responsible for the lower elevation of their curve compared to that of Scott *et al.* (1991) since a lowering of body temperature, which would occur under general anaesthetic, reduces TOBEC for a given lean mass (Scott *et al.*, 1991). There is no need to anaesthetise birds before measuring TOBEC since highly repeatable and rapid measurements can be taken from birds which are harmlessly restrained in some sort of jacket which retains them in a standard position.

Calibration and validation of TOBEC for estimating lipid mass

There has been much debate on the indirect use of TOBEC to estimate lipid mass in birds. Early studies (Castro *et al.*, 1990; Roby, 1991; Scott *et al.*, 1991) suggested deriving lipid mass by the deduction of PTLM (derived using regression models relating TOBEC to TLM) from BM (measured by weighing). However, subsequent studies (Morton *et al.*, 1991; Skagen *et al.*, 1993) pointed out that the absolute error in deriving PTLM and PFM is the same but is usually a greater proportion of the FM being estimated since TLM usually exceeds FM. They recommended the use of multiple regressions to estimate FM from BM and

TOBEC since the error associated with predicting FM is independent of that associated with predicting TLM.

In my study, estimation of FM by subtraction of PTLM from BM gave smaller errors than a multiple regression model with I and BM as independent variables. In the group of Redshank on which estimates of FM were calculated, FM ranged from 11.6-64.4g, over which a mean absolute error of 4.31g ± 2.51g (95% CI) had a resolution of 8.1% ± 4.7% (i.e. mean absolute error [FM - PFM] as a percentage of the range of FM being estimated).This level of resolution was sufficient when for example, comparing monthly mean PFM of Redshank throughout the non-breeding season when mean monthly PFM ranged between 8g and 47g (see Chapter 2). The mean change in PFM within individual Redshank brought into captivity was 12.4g. Therefore it can be concluded that the resolution of the predictive model of PFM developed in this study was sufficient for the context in which it was being used and the way in which the data has been interpreted statistically was robust enough to prevent errors of prediction interfering with the final interpretation of results.

Whereas multiple regression proved less effective at determining PFM in my study, other studies have used the technique to incorporate BM, TOBEC and various body size measurements to predict FM (Skagen *et al.*, 1993; Conway *et al.*, 1994; Meijer *et al.*, 1994). They used stepwise multiple regression to extract independent variables according to their contribution to overall variance in FM. Conway *et al.* (1994) concluded that TOBEC was not useful for estimating FM since it did not improve significantly the multiple regression model of FM based on BM, a fat score index and various body measurements. The use of stepwise multiple regression using supposedly independent variables which are not actually independent (e.g. body mass, TOBEC, wing-length, tail length etc. which are all inter-correlated) has been deemed inappropriate by James & McCulloch (1990). In a review of multivariate analysis in ecology they concluded that they "*could not* *find a single application of multiple regression to recommend as a good example"* and warned that stepwise multiple regression could not necessarily produce the best fitting or realistic model and could not be used consistently to extract the most important and influential variables. Therefore, the predictive models of FM in Skagen *et al.* (1993), Conway *et al.* (1994) and Meijer *et al.* (1994) should be used with caution, particularly that of Meijer *et al.* (1994), which was not tested by cross-validation techniques.

APPENDIX 3

ENERGY EXPENDITURE AND WEATHER CONDITIONS AT TEESMOUTH AND THE WASH

KEY TO UPPER GRAPH:

Bars:

lightly stippled - Total maintenance metabolism M_{maint} (KJ) per pentad (see section 3.2.4) of *robusta*

grey - Total M_{maint} of *britannica*

Lines:

dotted - Maximum sustainable level of M_{maint} of *robusta* (see section 3.2.4)

plain - Maximum sustainable level of M_{maint} of *britannica*

bold - Mean daily standard operative temperature T_{es}

KEY TO LOWER GRAPH:

Bars:

dark - mean daily wind speed (m/s)

white - maximum daily wind speed (m/s)

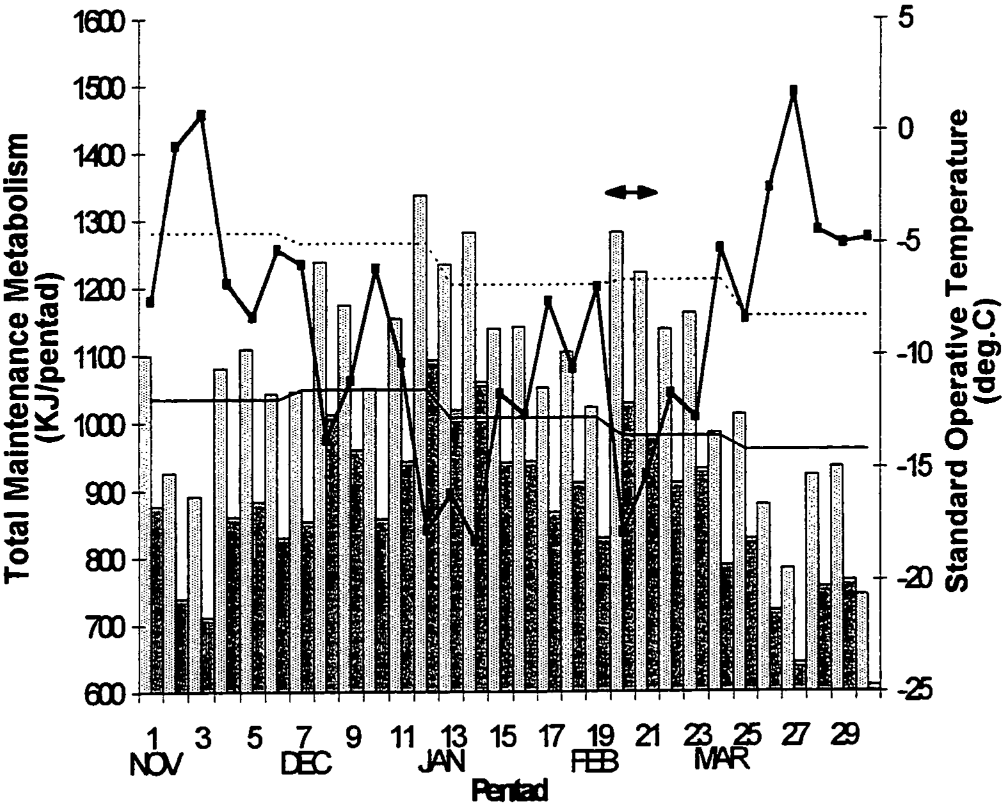
Lines:

plain - mean air temperature (°C)

dotted - minimum air temperature (°C)

Double arrows: indicate pentads which were associated with large-scale mortality of Redshank.

Figure A1: Teesmouth 1990/91



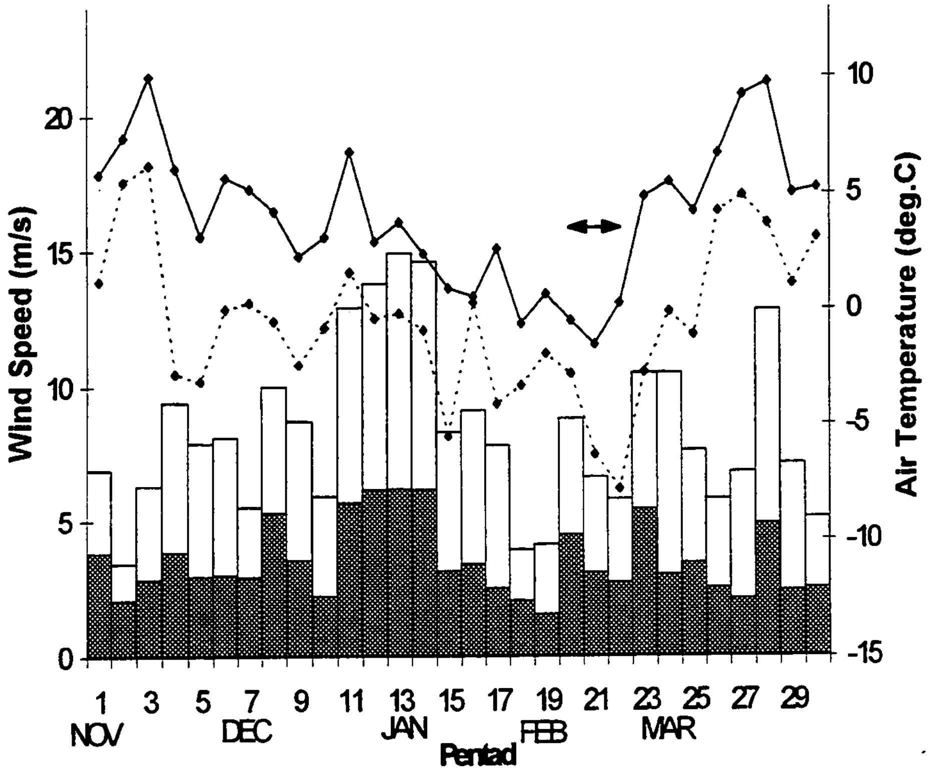
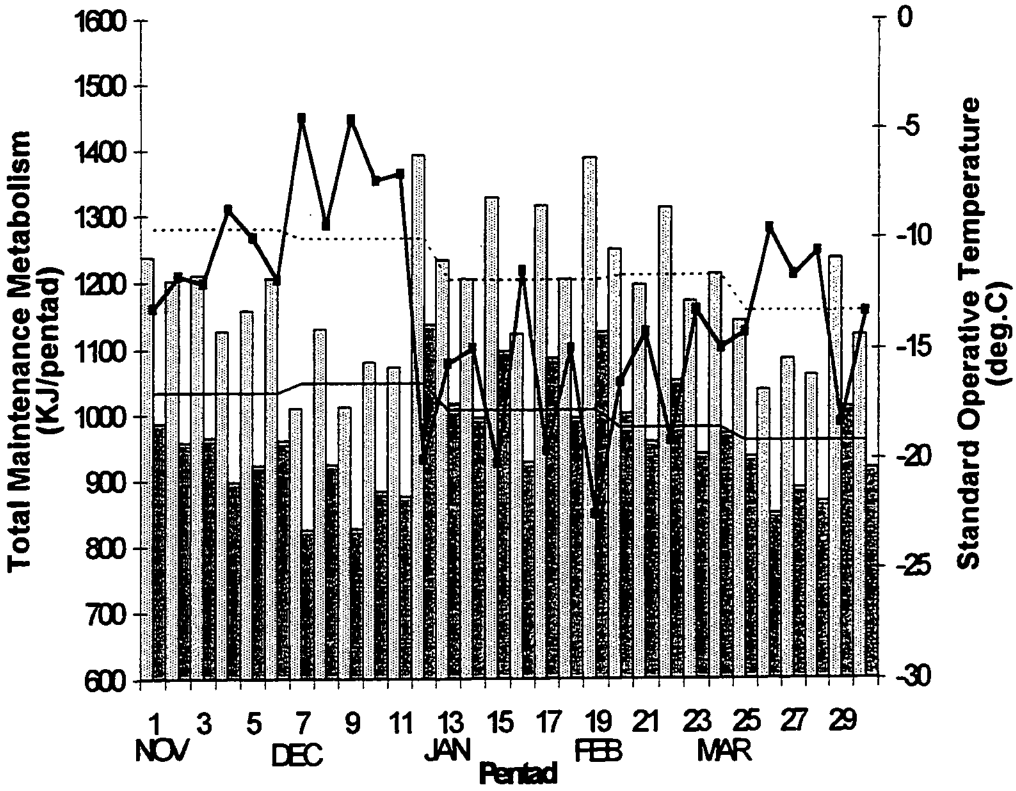


Figure A2: Teesmouth 1985/86



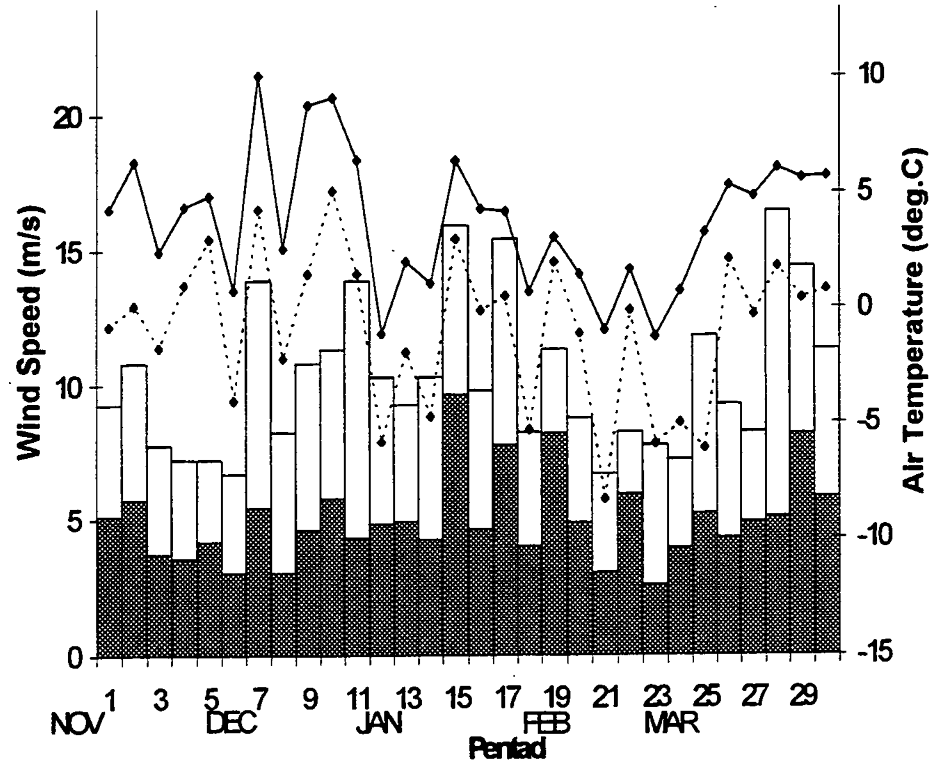


Figure A3: Teesmouth 1984/85

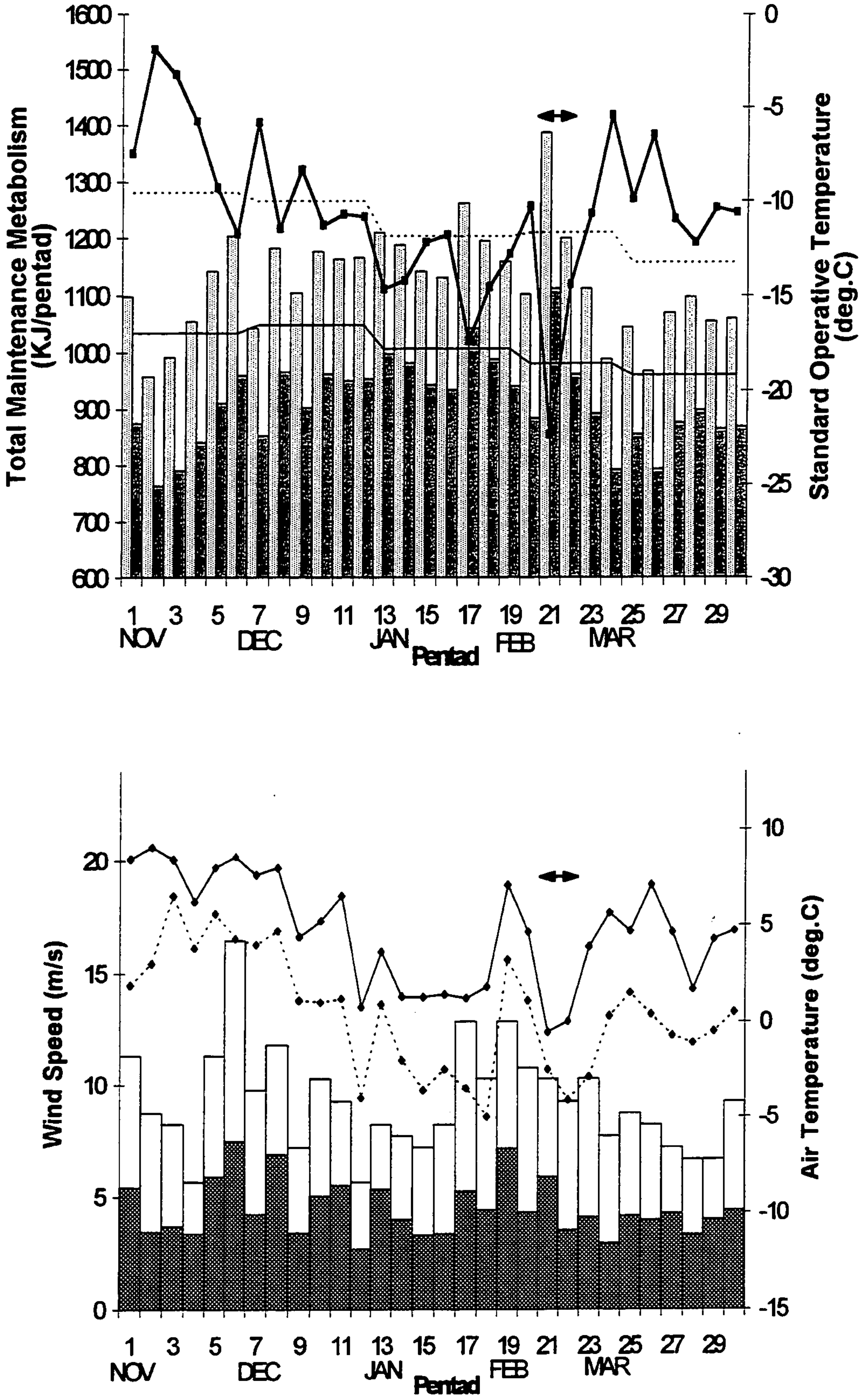
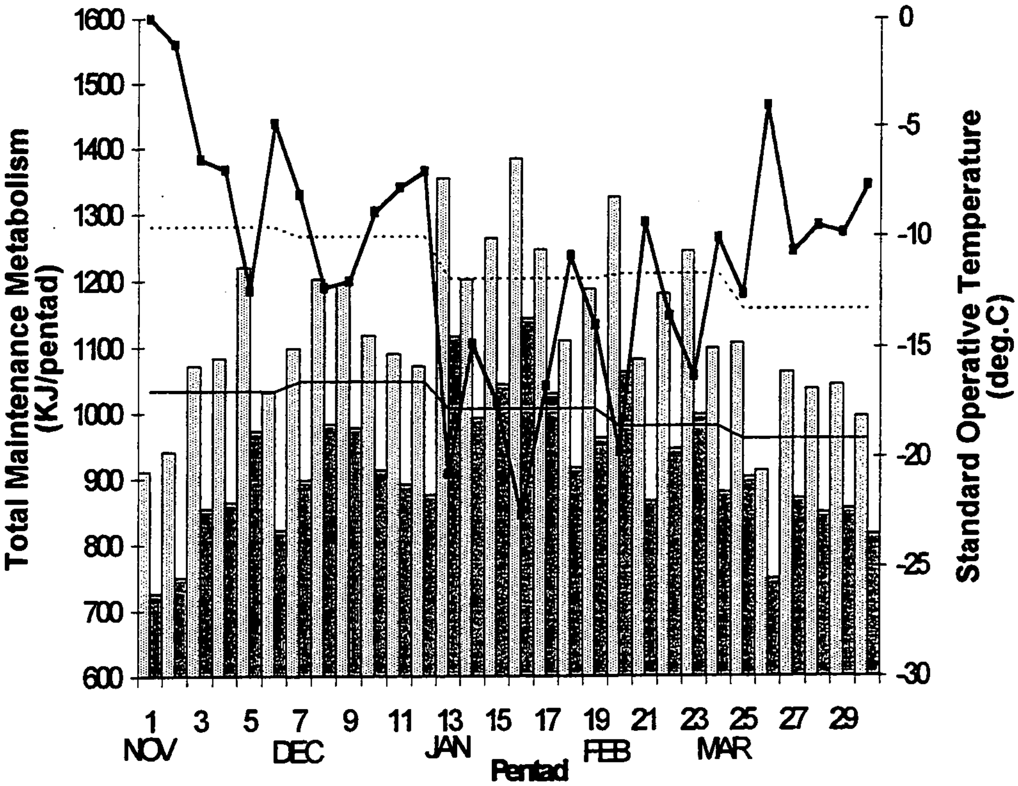


Figure A4: Teesmouth 1983/84



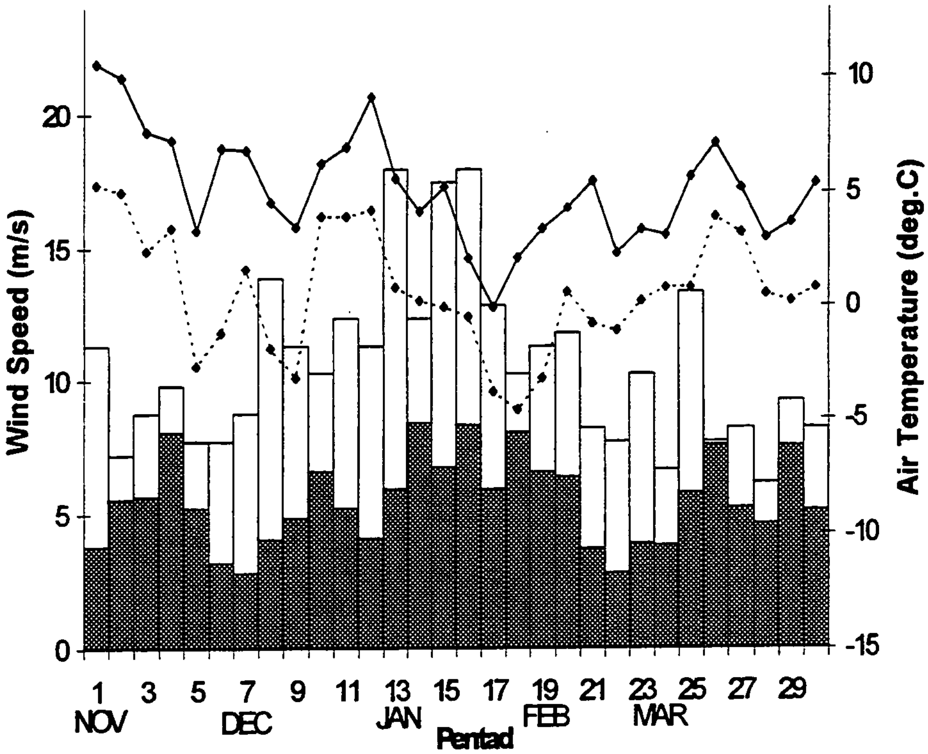
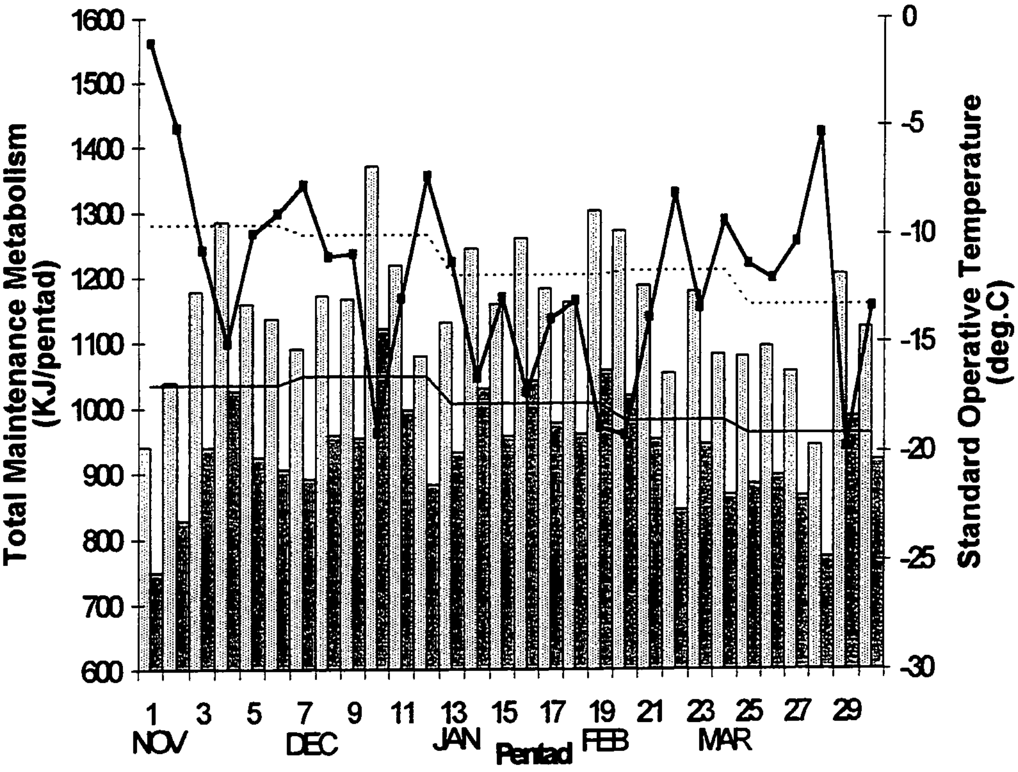


Figure A5: Teesmouth 1982/83



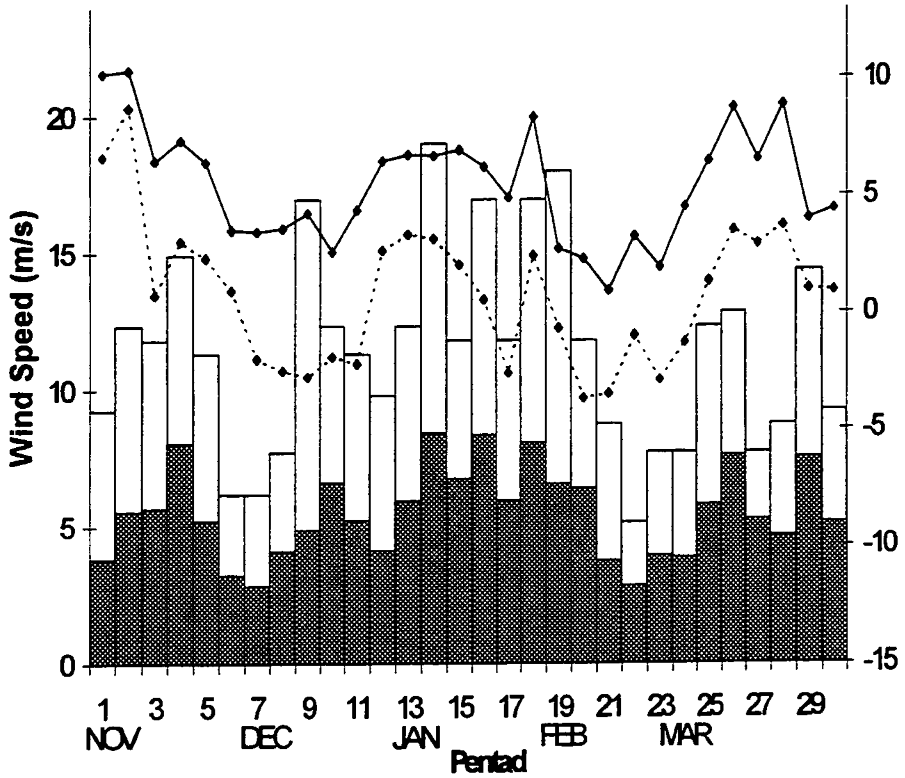


Figure A6: Teesmouth 1981/82

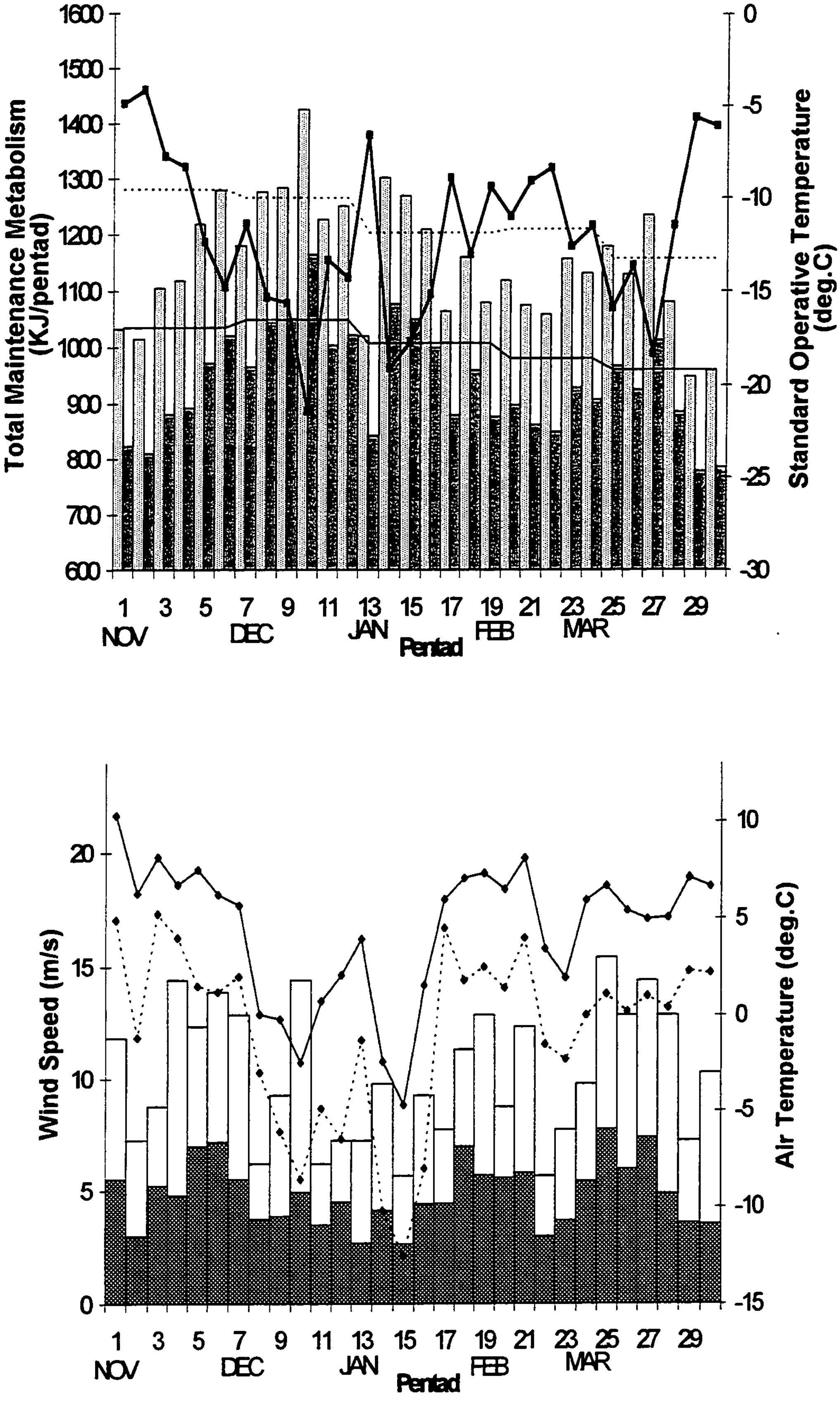
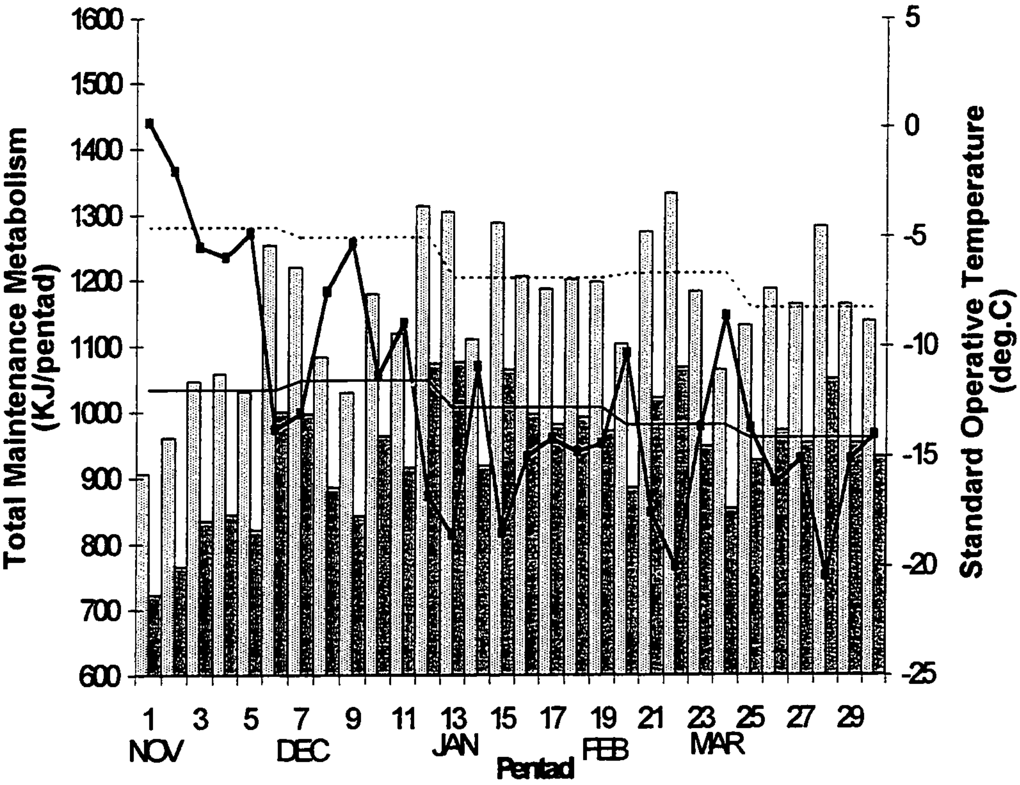


Figure A7: Teesmouth 1978/79



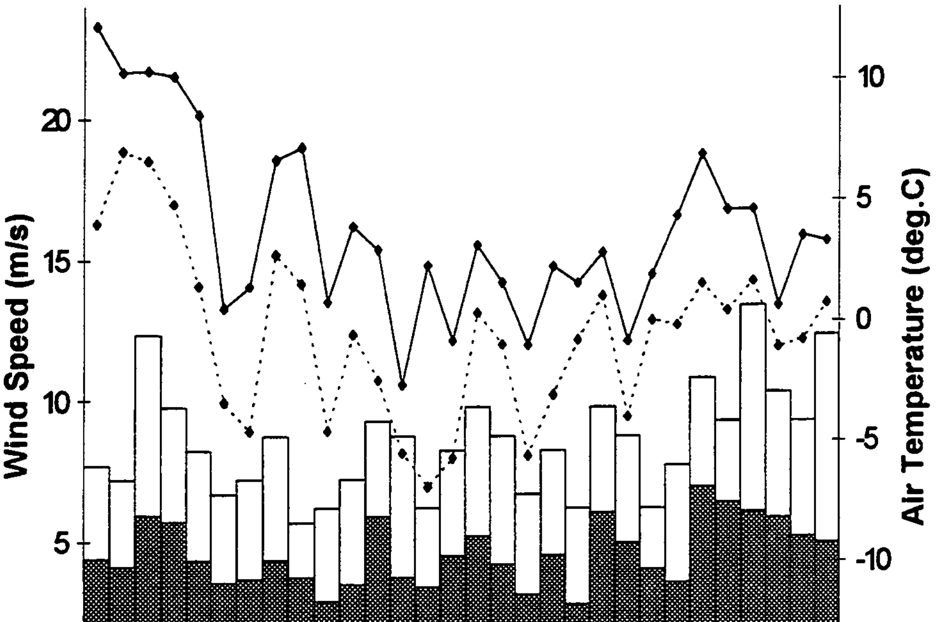


Figure A8: The Wash 1990/91

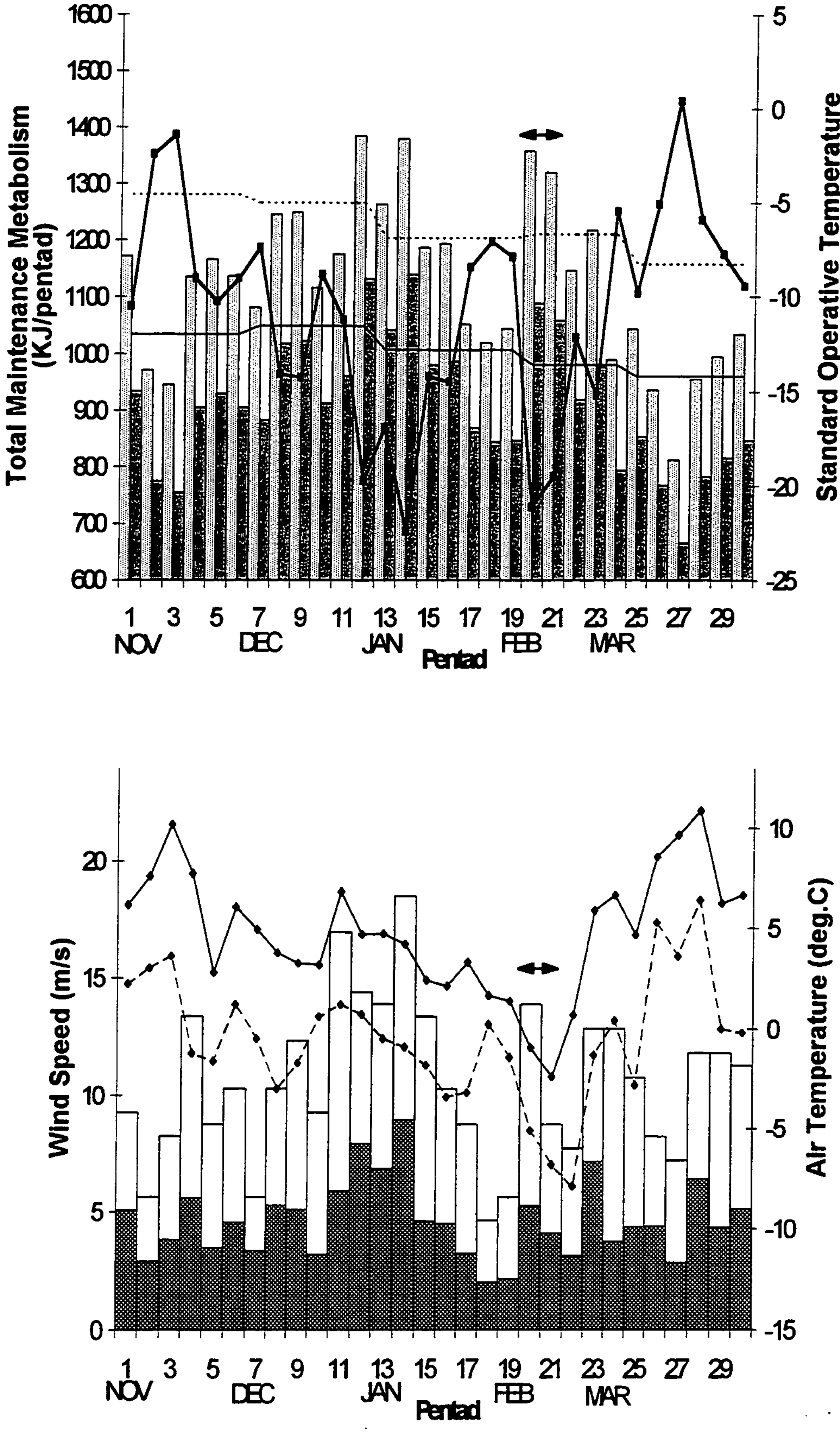
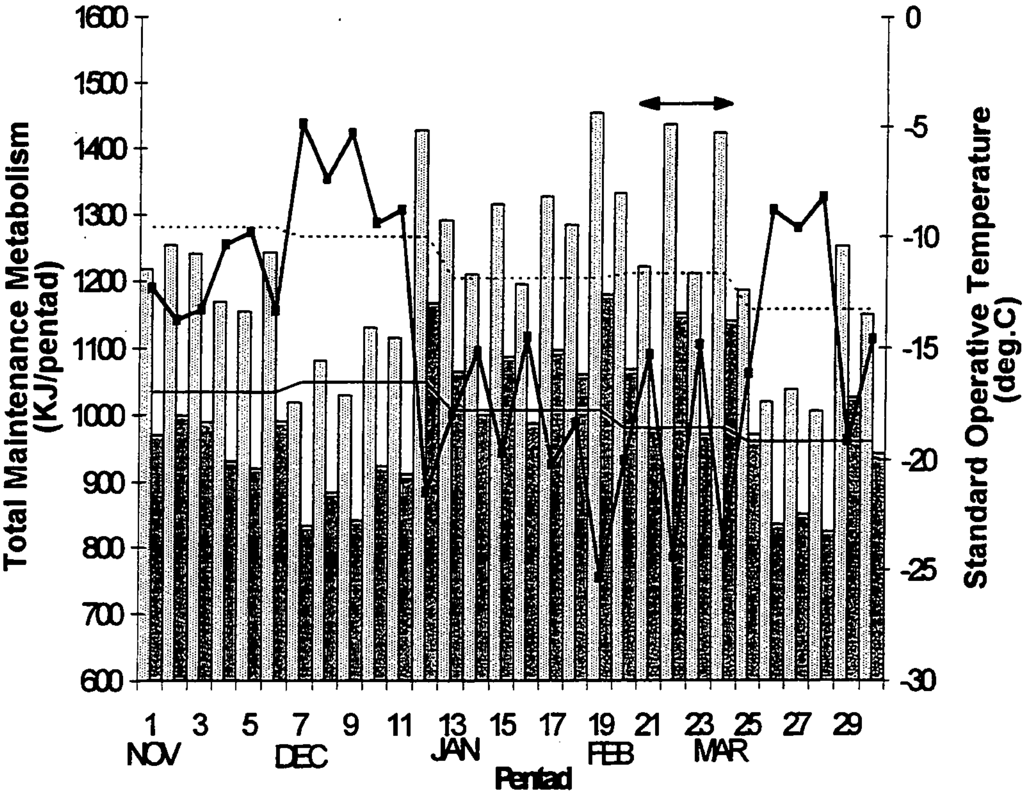


Figure A9: The Wash 1985/86



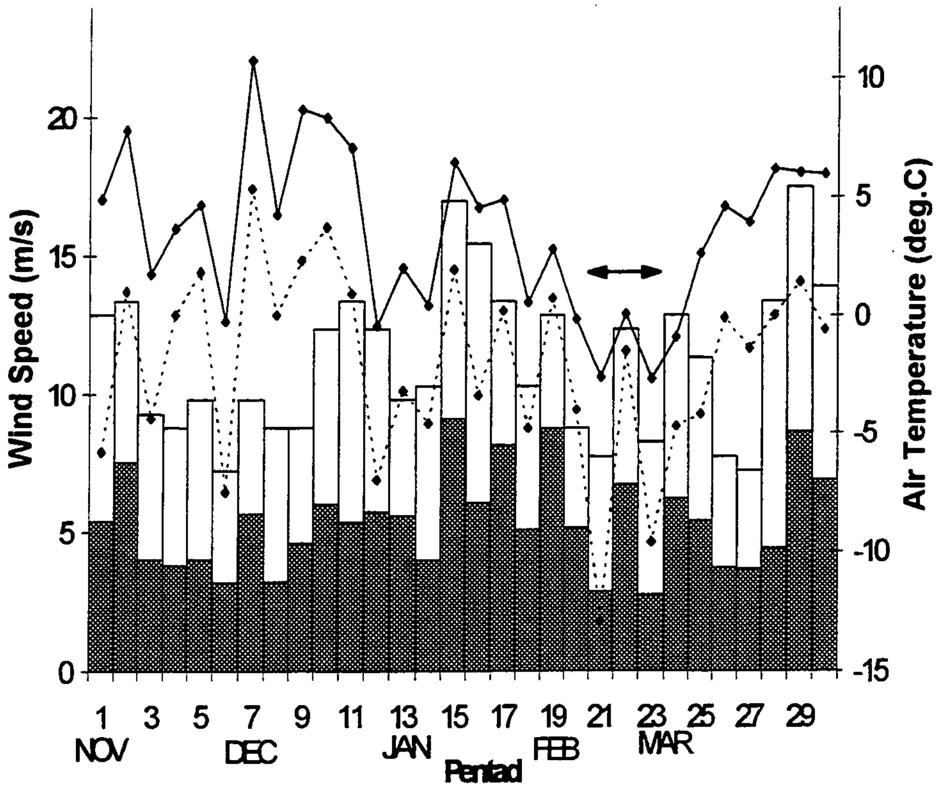
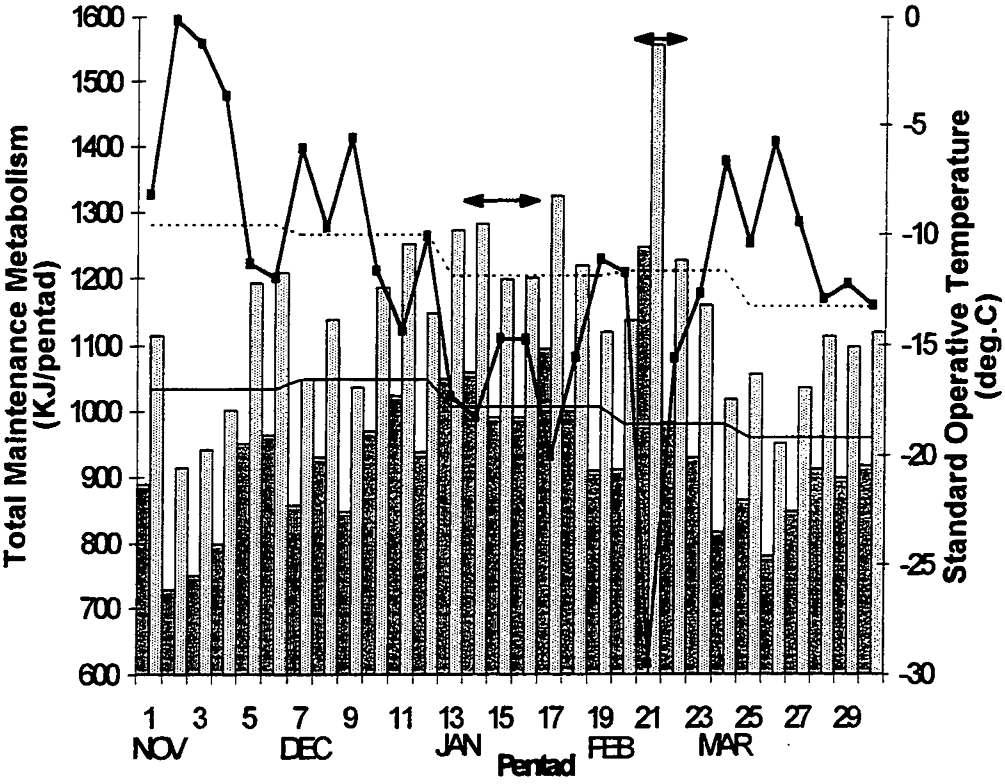


Figure A10: The Wash 1984/85



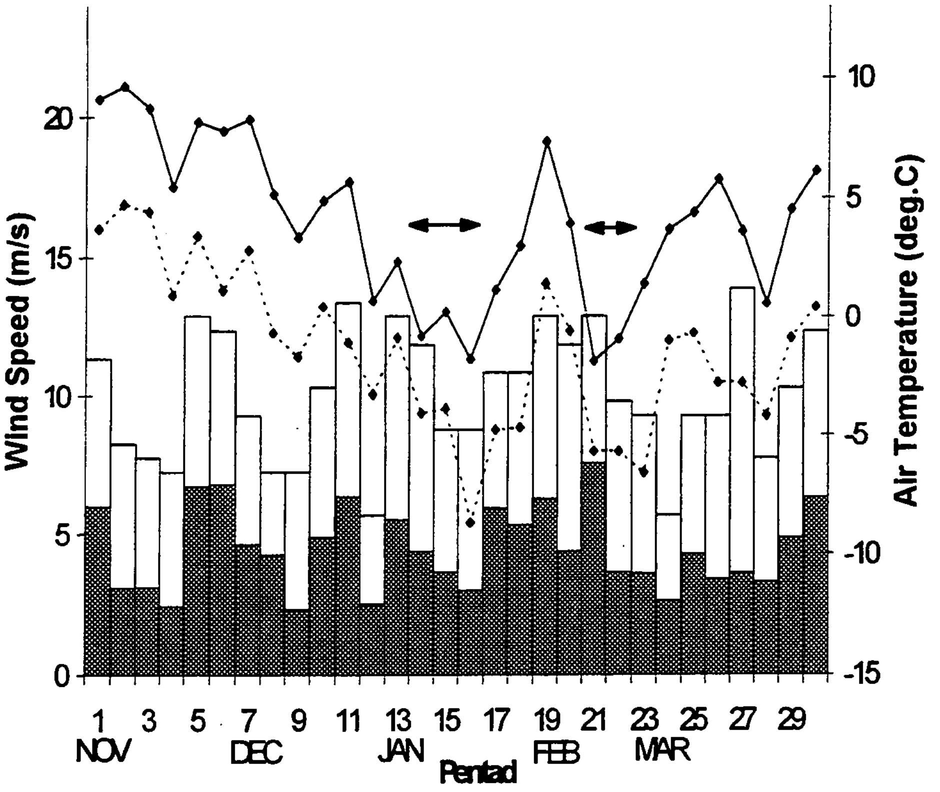
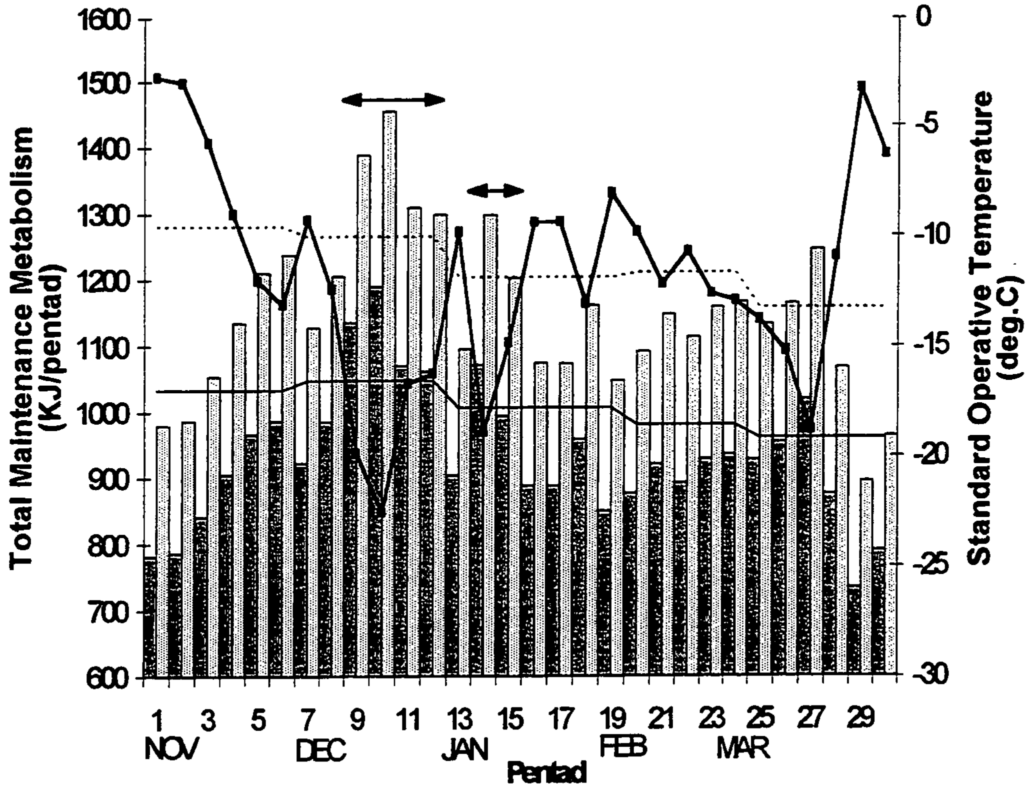


Figure A11: The Wash 1981/82



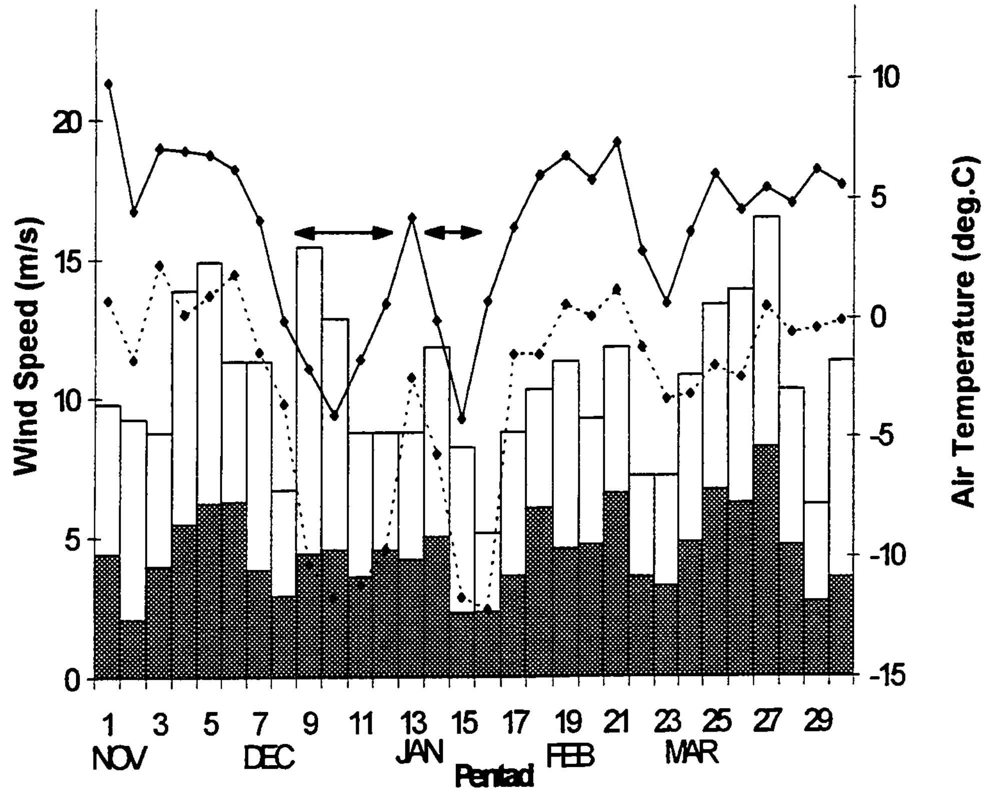
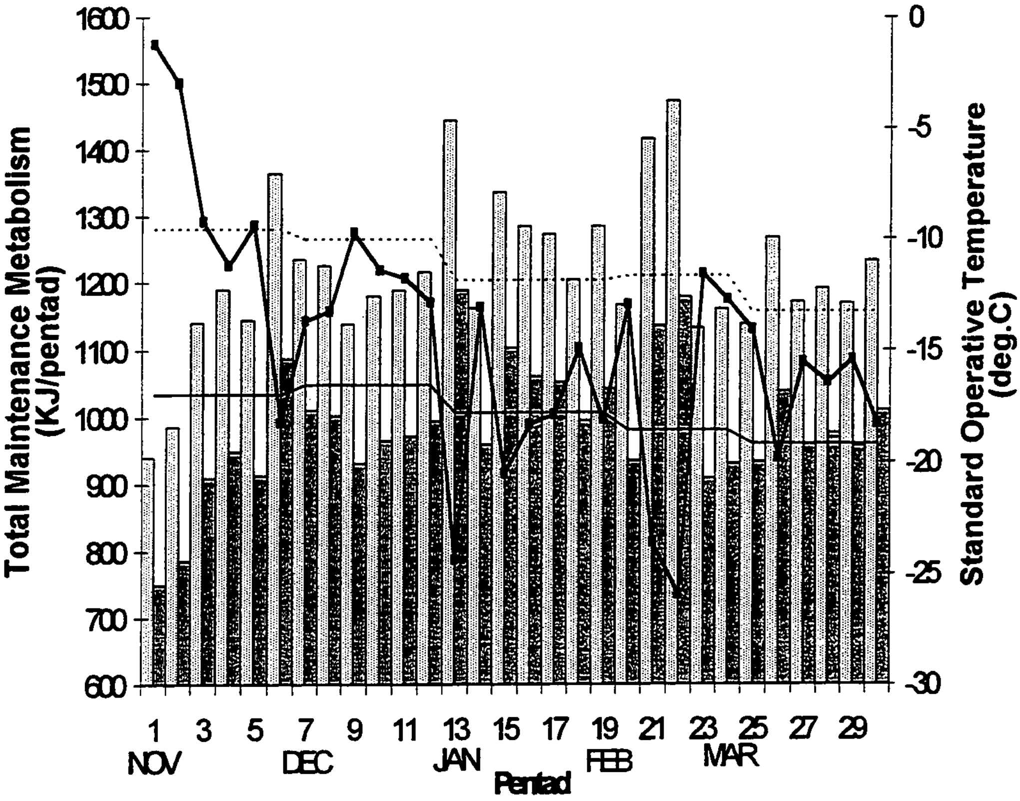
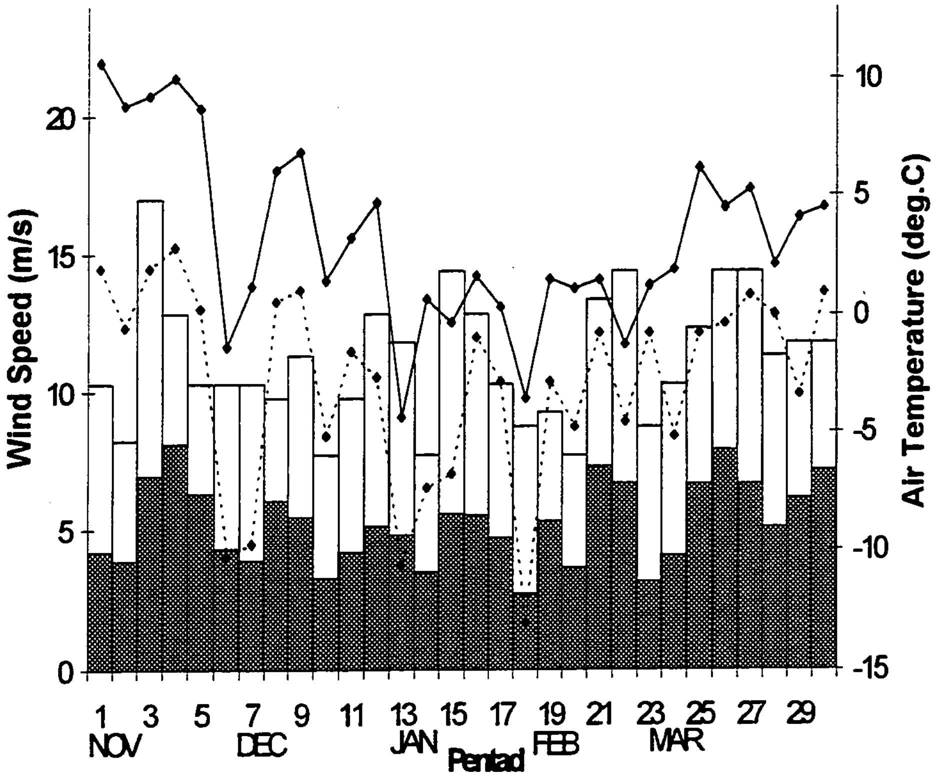


Figure A12: The Wash 1978/79





APPENDIX IV

Interactions between Redshank foraging behaviour, prey density, weather and energy demands

Introduction

Aims

This Appendix presents data from observations of all Redshank (including those of unknown race) at Teesmouth and against which, observations of *robusta* and *britannica* were compared in Chapter 3, in terms of a) seasonal changes in foraging rate parameters (i.e. pecking rate, pacing rate and paces per peck); b) the effects of ambient air temperature and wind speed on foraging rates; and c) the intake of large worms. It also summarizes studies of how Redshank respond to changes in energy demand for maintenance (i.e. M_{maint}) in terms of foraging rate, foraging time and intake of large worms.

Foraging and energy demands

Most studies of foraging shorebirds (e.g. Dugan, 1981; Goss-Custard, 1969; Pienkowski, 1983; Smith, 1975) have considered changes in food intake as functions of ambient weather conditions and prey density. Goss-Custard (1977b) and Speakman (1983) showed that Redshank maximised their rate of energy intake from their preferred prey by concentrating feeding in areas of the highest prey densities. Redshank feeding on *Nereis* optimised their rate of energy intake by taking only large worms when large worms were abundant in relation to smaller size-classes (Goss-Custard, 1977d&e). Speakman (1984) concluded that in winter Redshank do not maximise the rate of net energy gain in relation to the energy available from the prey present, confirming Goss-Custard's (1977a) finding that

Redshank prefer *Corophium* over *Nereis* despite the potential energy gain being much greater in the latter.

Speakman (1984) compared instantaneous rates of energy intake and energy expenditure whilst feeding. However, it may be that Redshank are regulating their food intake according to cumulative energy demands over several days. Redshank carry sufficient fat and protein reserves in winter to sustain them without food for several days (Chapter 5) and hence, on very cold days, they have the capability to supplement energy intake from food by drawing on reserves. These reserves will have to be replenished when conditions improve. Therefore food intake may be high on mild days following severe weather even though immediate energy demands are in fact low. My study examined how cumulative daily M_{maint} (predicted from heat loss of heated taxidermic mounts) affects foraging behaviour.

Methods

Foraging Behaviour

As explained in Chapter 4, food intake could not be measured directly. Instead, the foraging rates in terms of rates of pacing and pecking at cues were measured and used as an indication of food intake. The observations took place between October and March during the winters of 1993/94 and 1994/95. The methods employed to measure foraging rates are outlined in section 4.2.3.

The effect of weather and energy demand on foraging behaviour

Feeding rates were compared with measurements of windspeed and air temperature and with estimates of Maintenance Metabolism M_{maint}. Measurements of mean hourly windspeed (in m/s at 10m) and mean hourly air temperature (°C) were taken at Graythorp (data supplied by Hartlepool Borough

Council), 2km from Seal Sands. Details of daily sunshine hours were obtained from Tynemouth weather station (data supplied by the Meteorological Office) and converted into values of global solar radiation (see section 3.2.3). These meteorological data were incorporated into the Graythorp model for estimating M_{maint} derived in Chapter 3 using heated taxidermic mounts of Redshank. The model used for estimating M_{maint} is that for *robusta* rather than *britannica*, but this choice is inconsequential since the effects of temperature, wind speed and solar radiation are similar in the models of both races.

Flock time-budgets

During one observation day of each set of Spring tides, approximately hourly scans were made of Seal Sands from a single observation position, counting the number of Redshank which were either feeding, roosting, standing, preening or flying. More frequent counts were made between 2 and 6 hours after mean low water spring (MLWS) to determine when the majority of the Redshank feeding on Seal Sands had stopped feeding, if at all, with the approach of high water and the submergence of the mudflats. The median time at which the Redshank stopped feeding was defined as when more than half of the Redshank feeding on Seal Sands were either roosting, standing or preening, or had left the area to roost elsewhere. When birds did leave Seal Sands, they could often be seen heading for known roost sites and their presence was later confirmed by visits to these sites. Nearby fields and other known feeding sites were also checked for the presence of feeding Redshank, to check that the birds which had left Seal Sands were not feeding elsewhere.

Results

Seasonal changes in foraging behaviour

Figure 1 shows variation in pecking rate, pacing rate and paces per peck, both within and between each of the two winters studied. Pecking rate was significantly higher in 1993/94 (Kruskal-Wallis test $\chi^2_1 = 142.7$, $P<0.0001$) and both pacing rate and paces per peck were significantly lower (Kruskal-Wallis test $\chi^2_1 = 62.5$, $P<0.0001$ for pacing rate; $\chi^2_1 = 139.2$, $P<0.0001$ for paces per peck) in 1993/94 (n=223) than in 1994/95 (n=184). These inter-year differences were found in both races and were associated with a marked decline in the abundance of the preferred prey *Corophium* in 1994/95 (see section 4.3.3).

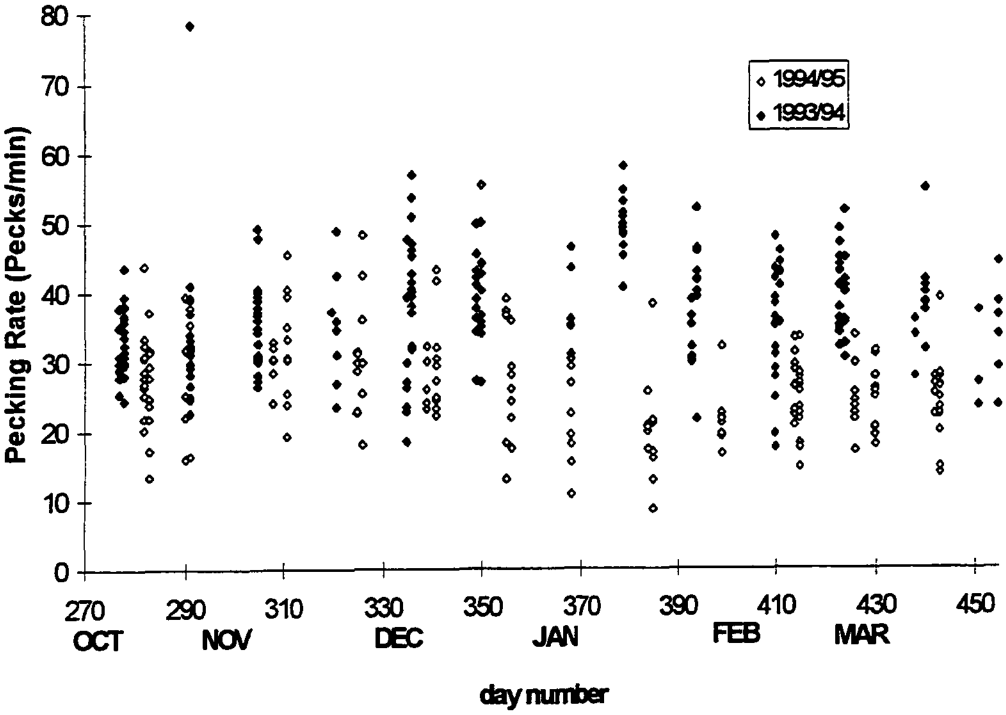
Within each winter there was significant variation in pecking rate, pacing rate and paces per peck with day number(Kruskal-Wallis test, see Table 1 for test statistics). In 93/94 pecking rate was higher and both pacing rate and paces per peck were lower in mid-winter than during October, early November and late March (Figure 1). In 94/95 however, the converse occurred (Figure 1).

The effect of ambient temperature and windspeed, and immediate energy demands (M_{maint}) on foraging behaviour

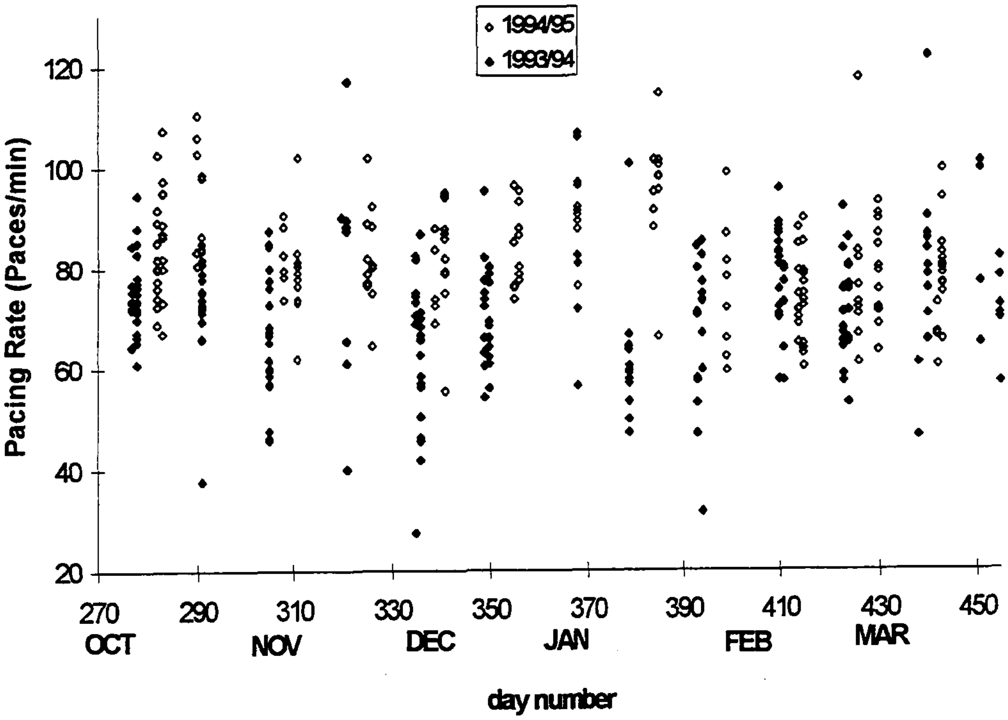
Pecking rates, pacing rates and numbers of paces per peck were compared to mean hourly air temperature and wind speed and estimated M_{maint} (in mW/g) at the time each observation was made. During the 1994/95 winter, Redshank showed a slight but significant reduction in pecking rate with increasing M_{maint} (Figure 2a; Table 2 shows Spearman rank correlation statistics). They also foraged less efficiently, in that the number of paces per peck, a measure of energy expended in foraging, increased significantly with increasing M_{maint} (Table 2 & Figure 2b).

Figure 1: Changes in a) pecking rate, b) pacing rate and c) paces per peck with day number during the winters of 1993/94 and 1994/95. (Day number 1 = 1 Jan 1993 or 1 Jan 1994 for the 1993/94 and 1994/95 winters respectively).

a) Pecking rate



b) Pacing rate



c) Paces per peck

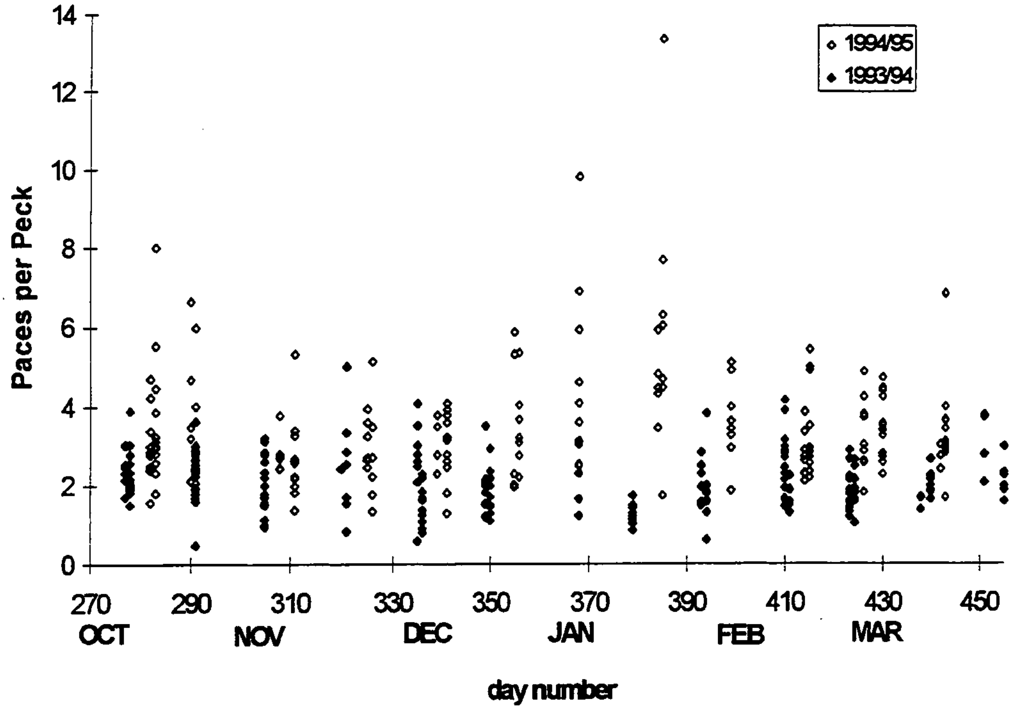
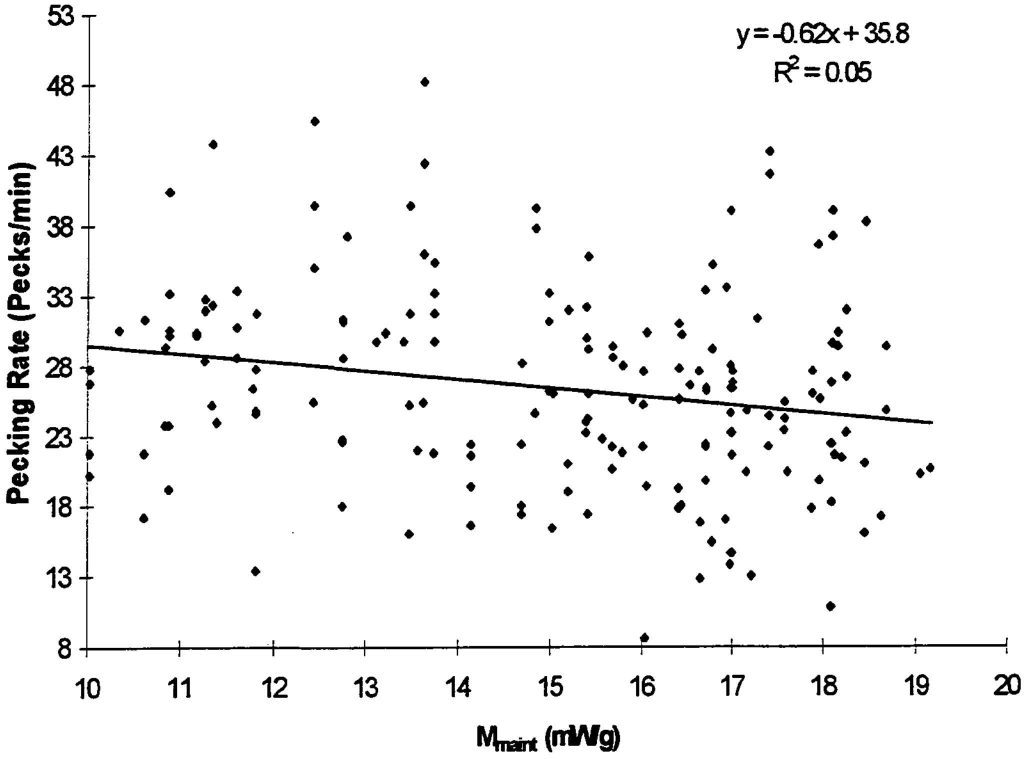


Figure 2: The effect of M_{maint} whilst feeding on a) pecking rate and b) paces per peck during the 1994/95 winter.

a) Pecking rate



b) paces per peck

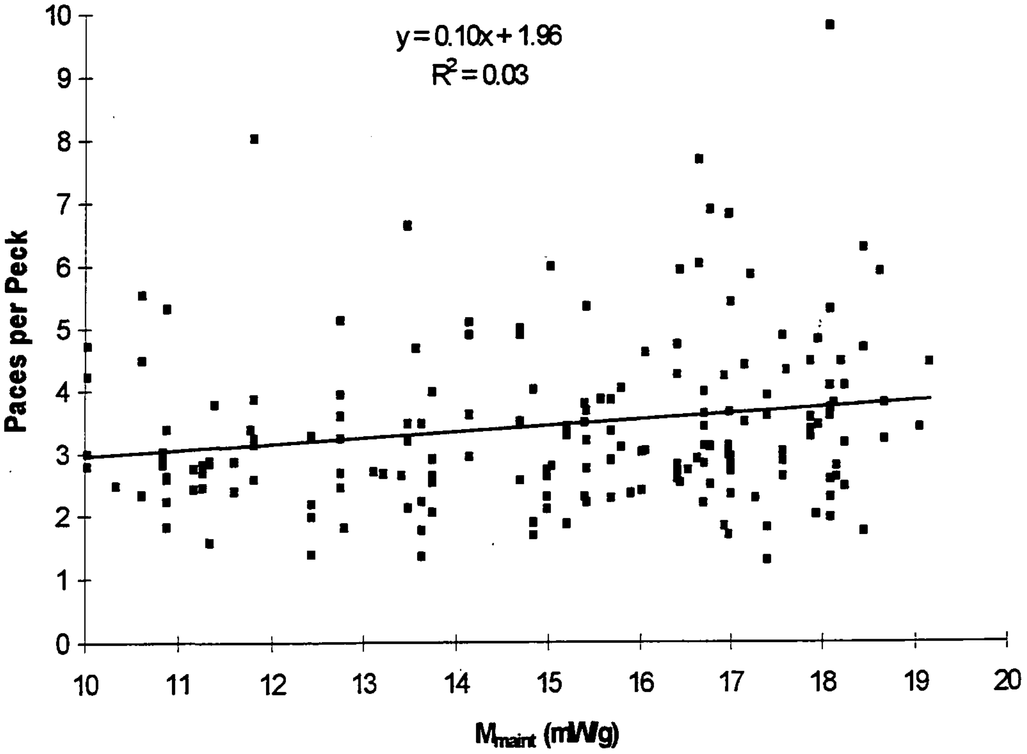


Table 1: Test statistics of Kruskal-Wallis test of the variation in foraging behaviour between days within the winters (Oct-Mar) of 1993/94 and 1994/95.

	χ^2_{21} **1993/94**	χ^2_{21} **1994/95**
Pecking Rate	87.7***	39.5 **
Pacing Rate	61.7***	57.5***
Paces per Peck	74.0***	35.0 *

*	significance level of $P<0.05$
**	significance level of $P<0.01$
***	significance level of $P<0.0001$

Table 2: Spearman rank correlation coefficients r_s for correlations of feeding behaviour of Redshank (n=184) with measurements of air temperature, wind speed and maintenance metabolism M_{maint} taken at the time of foraging observation during the winter (Oct-Mar) of 1994/95.

	air temperature	wind speed	M_{maint}
Pecking Rate	0.208 **	-0.163 *	-0.234 **
Pacing Rate	-0.186 *	-0.226 **	0.036 ns
Paces per Peck	-0.233 **	0.032 ns	0.192 **

ns	not significant
*	significance level of $P<0.05$
**	significance level of $P<0.01$
***	significance level of $P<0.001$

The reduced foraging efficiency at times of high M_{maint} resulted from the combined effect of low ambient air temperatures and high windspeeds whilst foraging (Figures 3 & 4). Pecking rate decreased significantly with decreasing air temperature (Figure 3a & Table 2), whilst the number of paces per peck increased significantly with decreasing temperature (Figure 3b & Table 2). Both pecking rate and pacing rate decreased significantly with increasing windspeed (Figure 4 & Table 2).

In contrast to the 1994/95 winter, Redshank foraging behaviour during the 1993/94 winter appeared to be independent of ambient temperature, wind speed and M_{maint} whilst foraging. Both pecking rate and paces per peck were not significantly correlated with either temperature, wind speed or M_{maint}. However, pacing rate increased significantly with falling air temperature (Spearman Rank Correlation r_s= -0.167 $P<0.05$), though not with wind speed or M_{maint}.

The effects of temperature and windspeed found in the total Redshank population at Seal Sands were mirrored by both races and the causes of these effects are discussed in section 4.3.2.

The effect of energy demand (M_{maint}) and temperature on preceeding days on foraging behaviour

Significant correlations were found in both winters between foraging behaviour and the levels of cumulative daily M_{maint} which the birds experienced over the previous 1-5 days (Tables 3 &4). However, the correlations in 1994/95 were in the opposite direction to those of the previous winter. In 1993/94 (Table 3), pecking rate was positively correlated with cumulative daily M_{maint} (Figure 5a) and, since pacing rate showed no correlation, the number of paces per peck decreased with increasing daily M_{maint} (Figure 6a). In 1993/94, pecking rate was also negatively correlated with cumulative hourly air temperature over 4 and 5 days (Table 5). Paces per peck was not significantly correlated with cumulative

Table 3: Spearman rank correlation coefficients r_s of correlations of pecking and paces per peck of Redshank (n=223) during 1993/94 with cumulative maintenance metabolism M_{maint} over one to five days before the feeding observation was made.

Number of days	Pecking Rate	Paces per Peck
1	0.286***	-0.228**
2	0.185 **	-0.143 *
3	0.223 **	-0.179**
4	0.244***	-0.177 **
5	0.281***	-0.223 **

ns	not significant
*	significance level of P<0.05
**	significance level of P<0.01
***	significance level of P<0.001

Table 4: Spearman rank correlation coefficients r_s of correlations of pecking rate and paces per peck of Redshank (n=184) during 1994/95 with cumulative maintenance metabolism M_{maint} over one to five days before the feeding observation was made.

Number of days	Pecking Rate	Paces per Peck
1	-0.306***	0.257***
2	-0.276***	0.237 **
3	-0.301***	0.228 **
4	-0.271***	0.206 **
5	-0.270***	0.189 *

ns	not significant
*	significance level of $P<0.05$
**	significance level of $P<0.01$
***	significance level of $P<0.001$

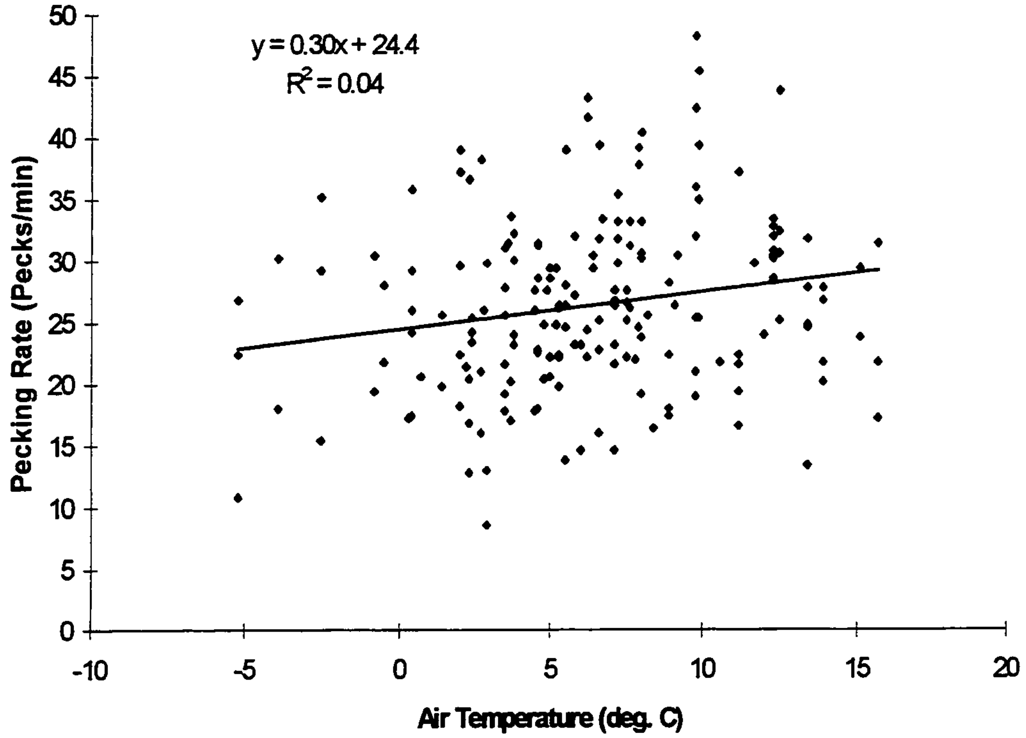
Table 5: Spearman rank correlation coefficients r_s of correlations of pecking rate and paces per peck of Redshank (n=223) during 1993/94 with cumulative hourly air temperature over one to five days before the feeding observation was made.

Number of days	Pecking Rate	Paces per Peck
1	-0.088 ns	-0.016 ns
2	-0.103 ns	0.037 ns
3	-0.123 ns	0.059 ns
4	-0.201 **	0.124 ns
5	-0.199 **	0.117 ns

ns	not significant
**	significance level of $P<0.01$

Figure 3: The effect of air temperature whilst feeding on a) pecking rate and b) paces per peck during the 1994/95 winter.

a) Pecking rate



b) Paces per peck

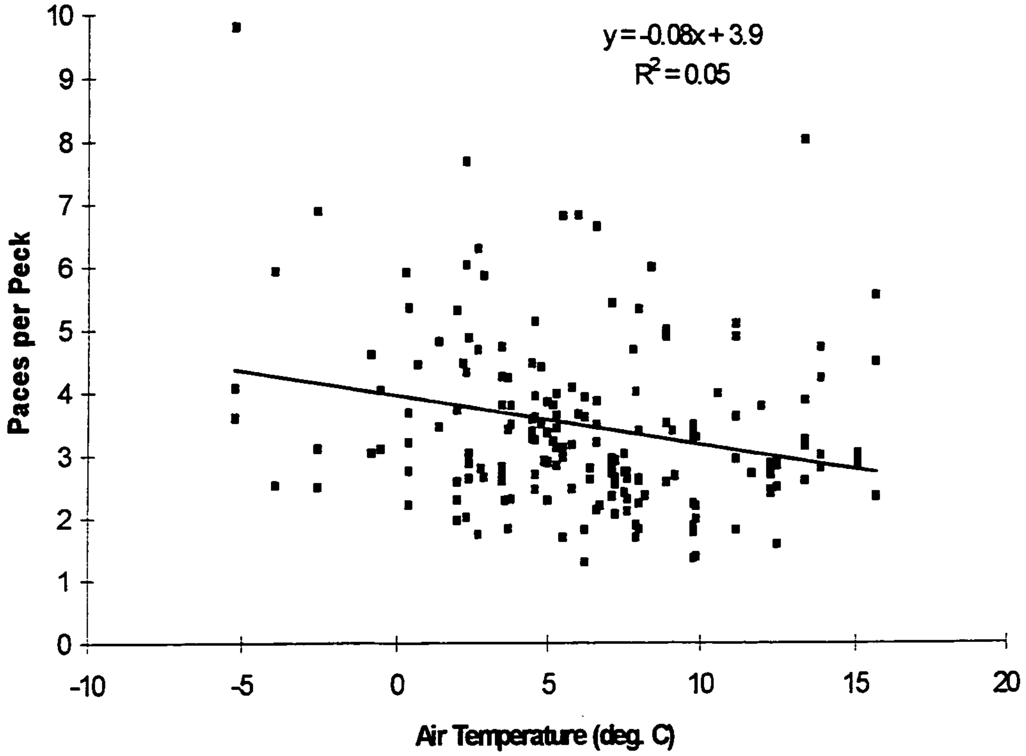
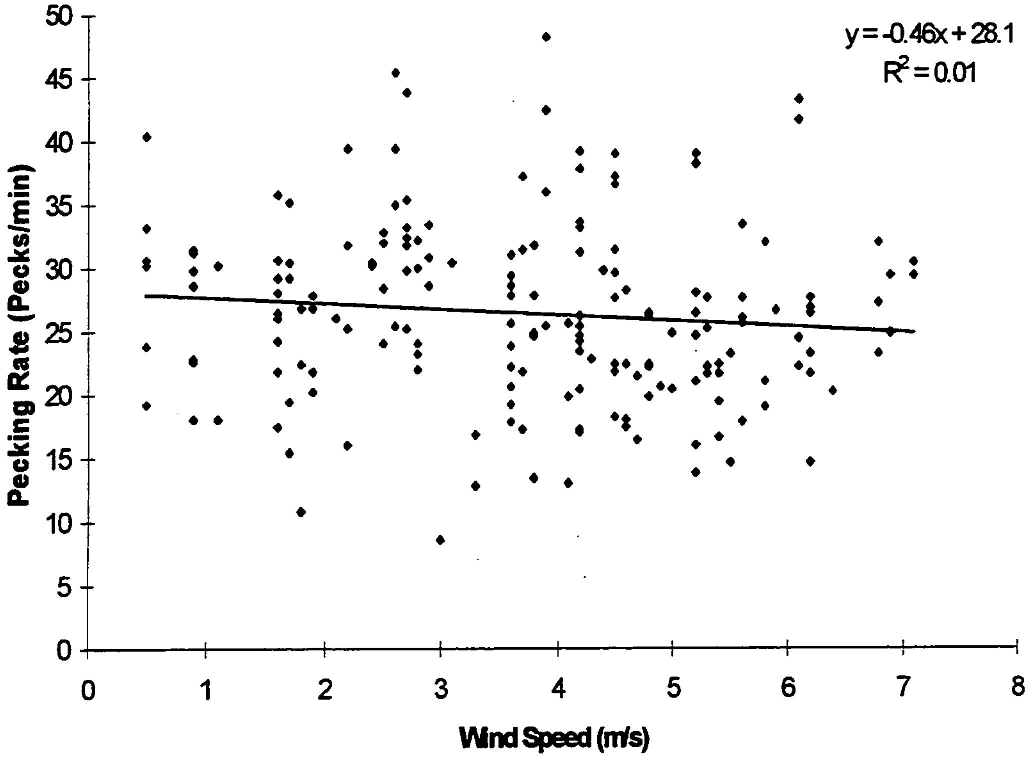


Figure 4: The effect of wind speed whilst feeding on a) pecking rate and b) pacing rate during the 1994/95 winter.

a) Pecking rate



b) Pacing rate

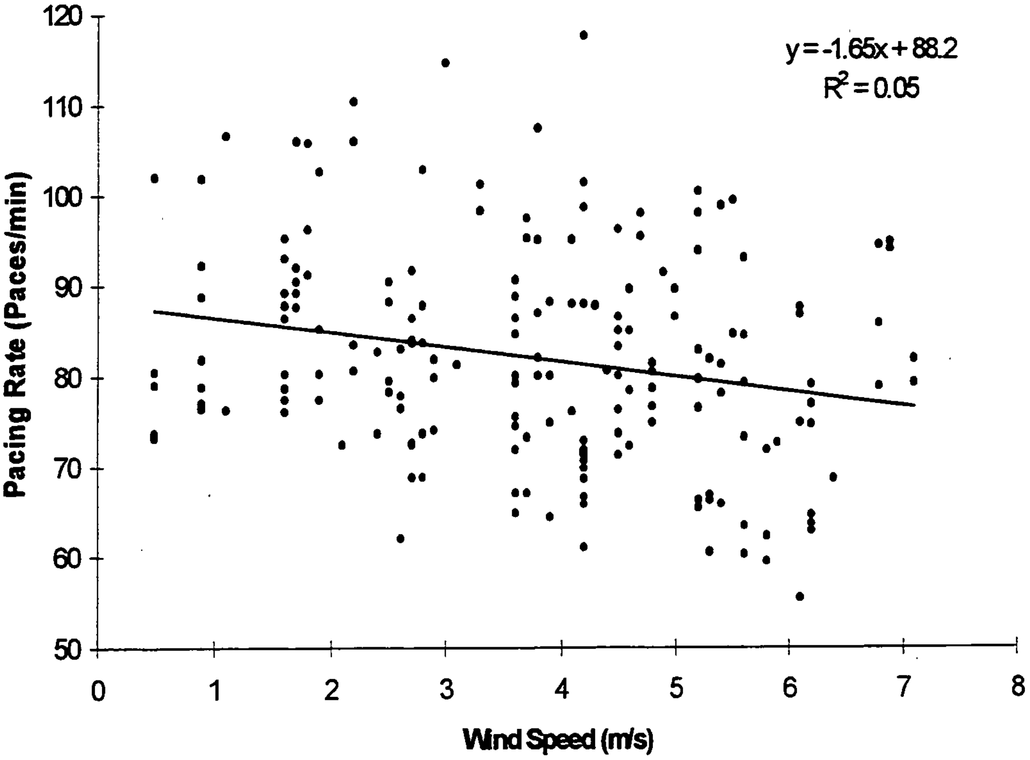
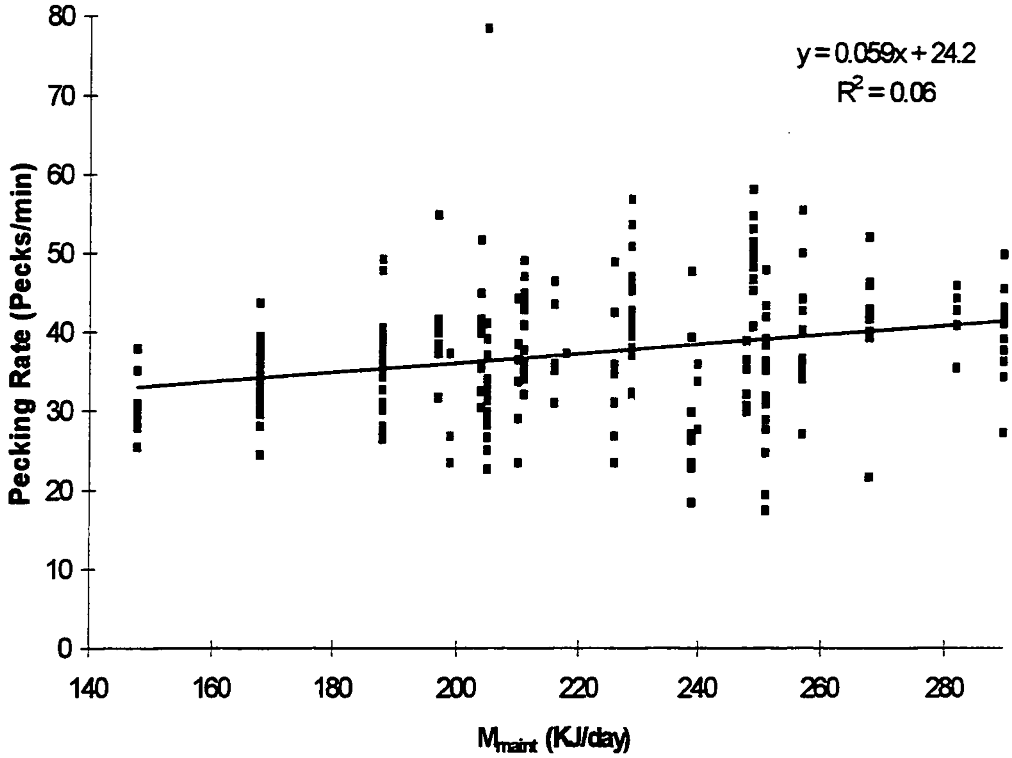
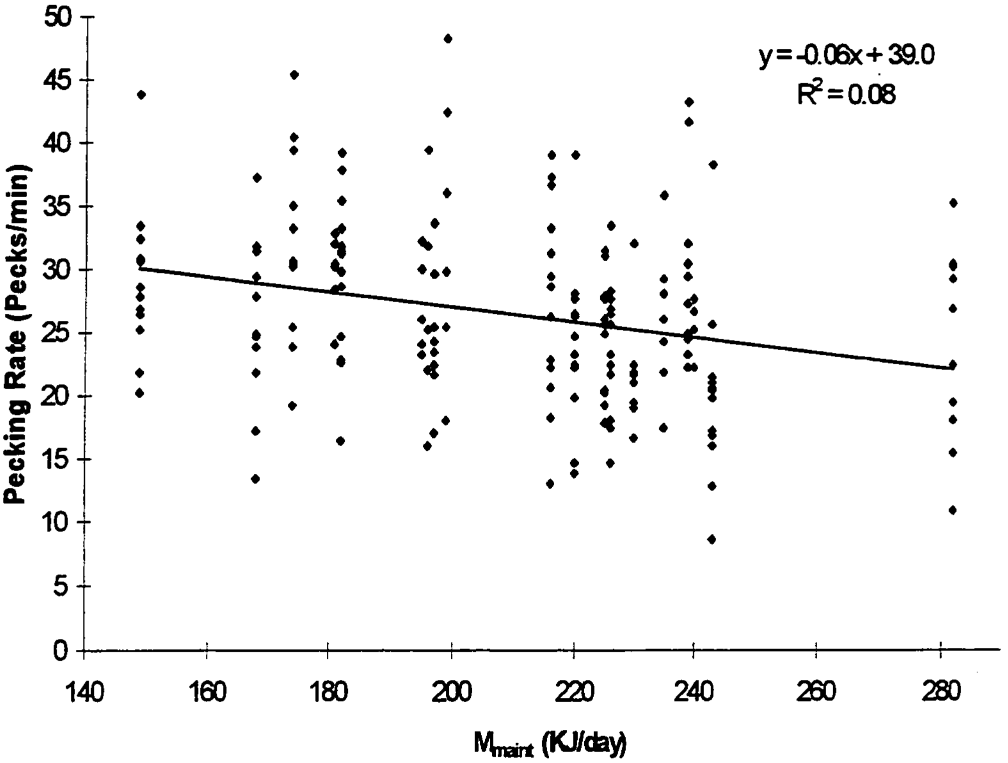


Figure 5: The effect of total daily M_{maint} one day before feeding observation on pecking rate during the winters of a) 1993/94 and b) 1994/95.

a) 1993/94



b) 1994/95



temperature, though r_s was positive and increased as temperature was accumulated over more days (Table 5).

In contrast, during 1994/95 pecking rate was negatively correlated with daily M_{maint} (Figure 5b; Table 4) whilst the number of paces per peck was positively correlated with daily M_{maint} (Figure 6b; Table 4). The correlation between pecking rate and cumulative hourly air temperature was positive and significant over 1-5 days before foraging was observed (Table 6). Paces per peck was significantly negatively correlated with cumulative hourly air temperature over 1-5 days (Table 6).

Numbers of larger prey items taken

On the whole, few large items featured in the diet of Redshank at Seal Sands during either of the two winters studied. Of those large items seen to be taken, worms predominated. During 1993/94 only 1 bird out of 223 was seen taking a large item other than a worm, a small crab (*Carcinus maenus*). During 1994/95, out of 184 birds observed, 2 birds were seen taking single bivalve molluscs, a third took 2 bivalves and a fourth took a small crab.

The maximum number of worms taken by a single indiviual in 5 minutes of observation was 6 in both winters. However, significantly more worms were taken per bird in 5 minutes during 1994/95 (mean=0.27 SE=0.068) than in 1993/94 (mean=1.09 SE=0.235) (Kruskal Wallis ANOVA χ^2_1 = 8.99 $P<0.01$).

During 1994/95 the mean number of worms taken per 5 minutes per bird increased as winter progressed (Figure 7a) and was significantly positively correlated with day number (Spearman rank rs=0.61 $P<0.05$), where day number equalled 1 on 1 January 1993. In 1993/94 the number of worms taken was not correlated with day number since worms were present in the diet only in mid-winter and almost absent at other times. This seasonal pattern of taking worms in 1993/94 was associated

Table 6: Spearman rank correlation coefficients r_s of correlations of pecking rate and paces per peck of Redshank (n=184) during 1994/95 with cumulative hourly air temperature over one to five days before the feeding observation was made.

Number of days	Pecking Rate	Paces per Peck
1	0.341***	-0.277***
2	0.319***	-0.250 **
3	0.283***	-0.223 **
4	0.323***	-0.254 **
5	0.323***	-0.258***

** significance level of $P<0.01$

*** significance level of $P<0.001$

with a significant correlation between the mean number of worms taken per bird and cumulative daily M_{maint} (Table 7). This correlation became stronger as daily M_{maint} was accumulated over more days and was significant only after 4 and 5 days (Table 7; Figure 7b). In contrast, during 1994/95 the number of worms taken may have decreased with cumulative daily M_{maint} (Figure 7b) though was significant with a probability of only 0.055 (Table 7) even after 5 days.

Time Spent Foraging

The individuals which made up the Redshank flock at Seal Sands numbered between 120 and 620 in 1993/94 and between 140 and 750 in 1994/95, and were well synchronized in their activities. When the majority were foraging, less than 10% were preening, roosting or standing. During the day (when this study was conducted) the majority of birds were foraging from at least 2 hours before MLWS until between 2h and 4h 24min in 1993/94 and between 2h 6min and 4h 13min after Low Water in 1994/95. The time at which the flock stopped feeding (measured in minutes after MLWS) was negatively correlated in both years with the daily M_{maint} the day before foraging was observed (Figure 8) (Spearman Rank correlation $r_{s,11} = -0.643$ in 1993/94, $r_{s,13} = -0.693$ in 1994/95, $P<0.05$). The relationship between foraging time and M_{maint} was the same (MANOVA $P>0.05$) in each winter studied. The Redshank at Seal Sands were, therefore, spending less time foraging during the day when cumulative energy demands for M_{maint} were high.

Discussion

Foraging Rates

In 1993/94 when densities of *Corophium* were high , behaviour appeared to be less dependant on immediate conditions, but more dependant on longer -term

Table 7: Spearman rank correlation coefficients r_s for correlations between the daily mean number of worms taken per bird in a 5 minute period and daily M_{maint} accumulated over 1-5 days before the observation was made, during 1993/94 (n=14) and 1994/95 (n=21).

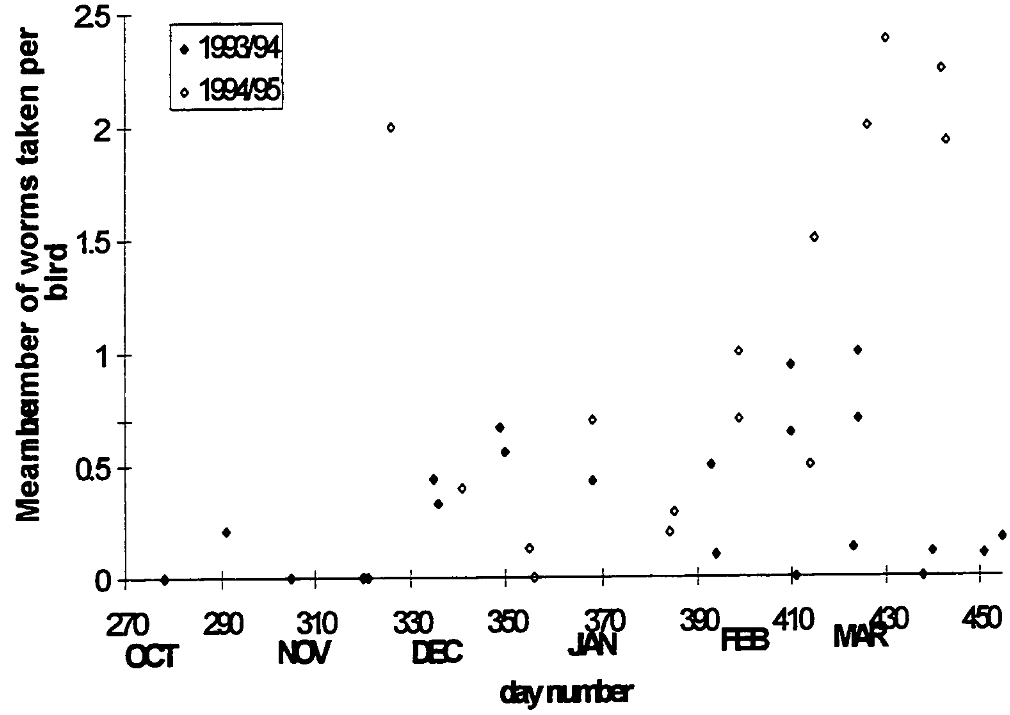
No. days	1993/94	1994/95
1	0.347 ns	-0.337 ns
2	0.354 ns	-0.086 ns
3	0.414 ns	-0.013 ns
4	0.459 *	-0.293 ns
5	0.441 *	-0.524 †

* $P < 0.05$

† $P = 0.055$

Figure 7: Variation in the mean number of worms taken per bird in 5 minutes with a) day number and b) Cumulative daily M_{maint} 5 days before observation.

a)



b)

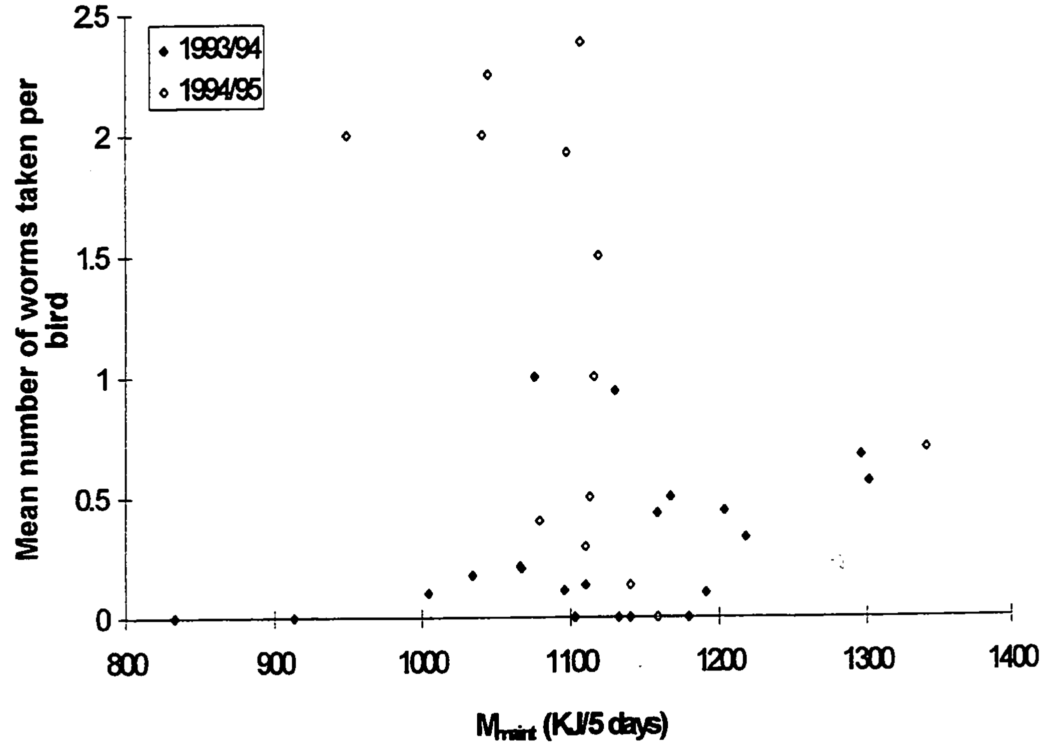
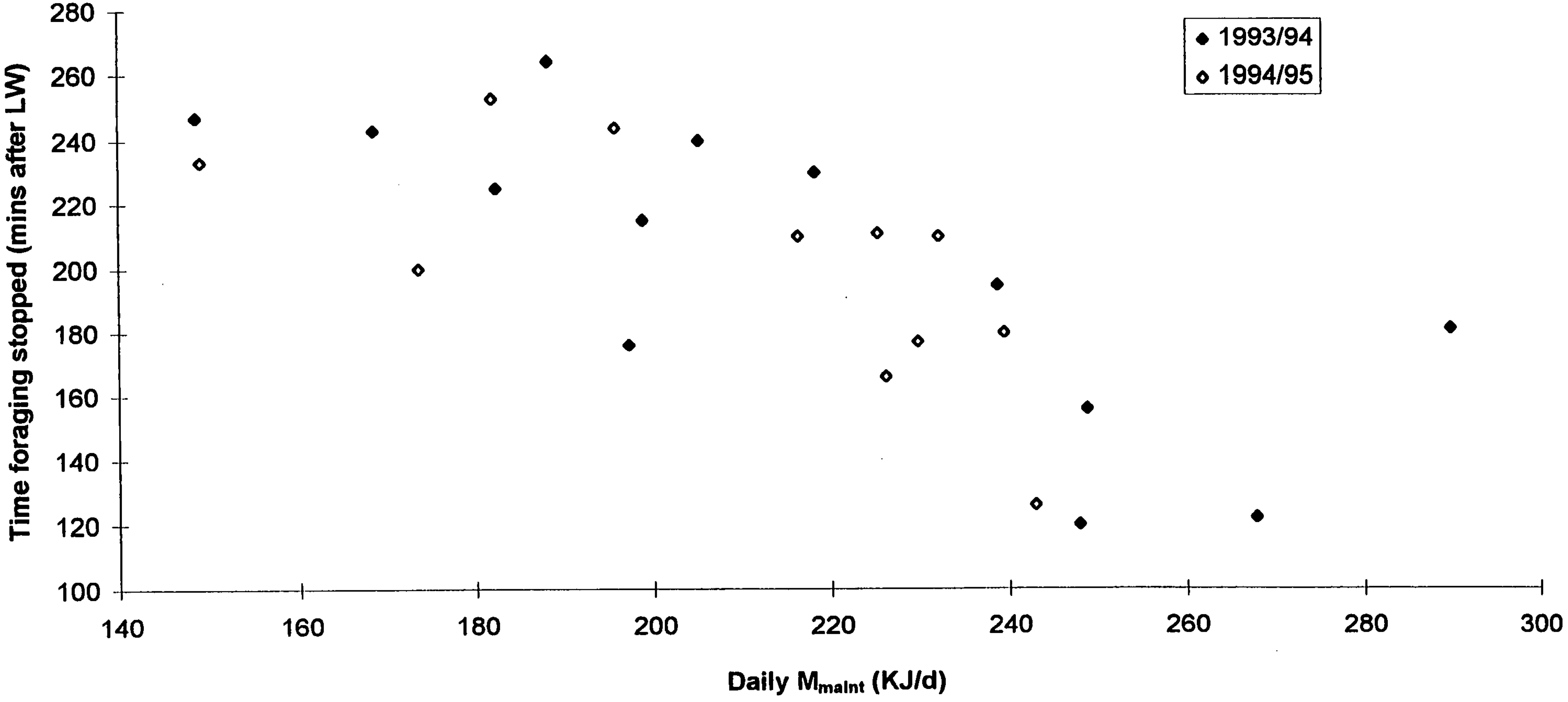


Figure 8: Effect of daily M_{maint} on the day before foraging of Redshank was observed on the time after Low Water (LW) that foraging stopped.



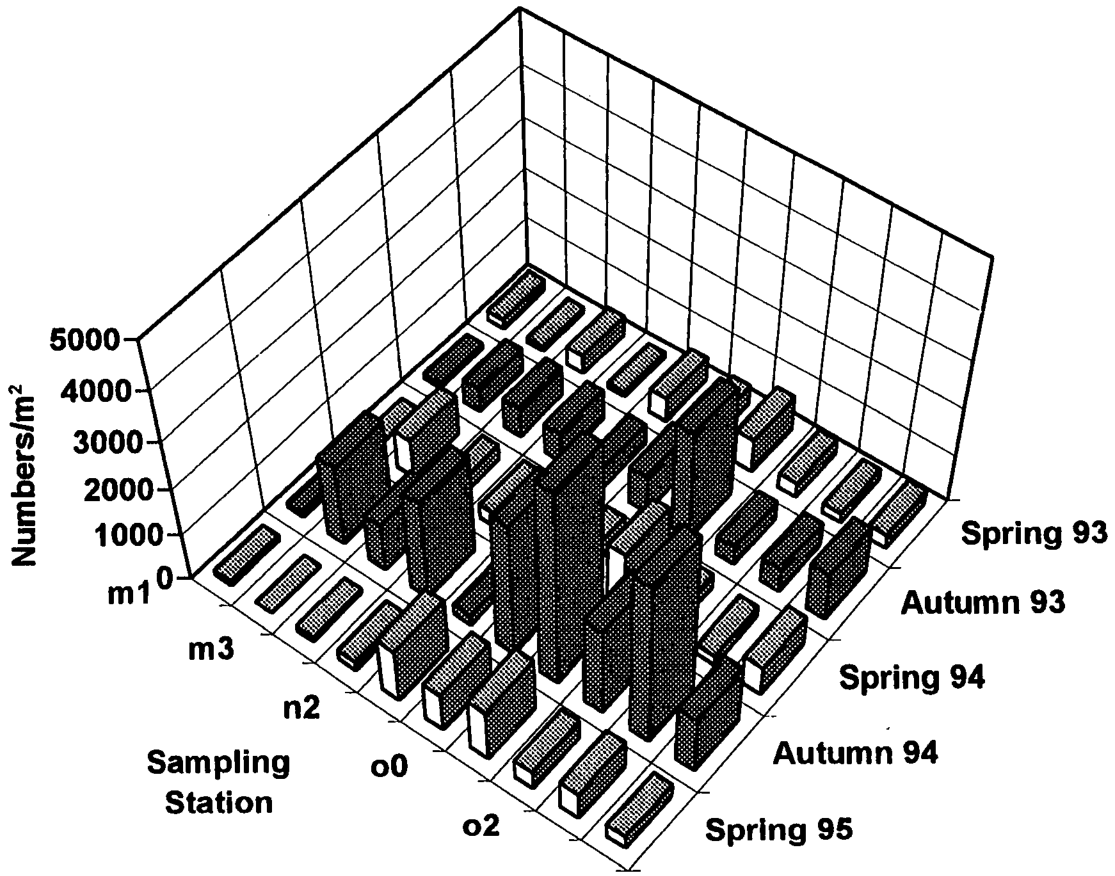
cumulative energy demands. It could be argued that periods of high M_{maint} coincided with high windspeeds but warm temperatures during which prey availability was still relatively high and, therefore, so was pecking rate. However, pecking rate was negatively correlated with cumulative hourly temperatures, significantly so over 4 and 5 days, suggesting that pecking rate did increase even when temperatures (and in turn, prey availability) were low. It is unlikely that the number of cues to which Redshank could respond were increasing as temperature decreased, since all existing evidence (e.g. Goss-Custard, 1969; Pienkowski, 1984; Speakman, 1984) suggests otherwise. It could be that in 1993/4, during periods of high M_{maint}, Redshank were pecking at cues that they would otherwise have ignored under more favourable conditions, when a greater number of positive cues (i.e. those indicating a greater chance of successfully encountering a prey item) would be present. It could be that although Redshank always aim to maximise food intake by feeding in areas of highest prey availability and/or density (Goss-Custard, 1977c; Speakman, 1983), they do so by optimising pecking rate and the energy expended when attempting to feed. It is reasonable to suggest that Redshank choose to respond to some cues, yet ignore others and not merely peck at everything they see, since Goss-Custard (1977d&e) demonstrated that Redshank are capable of choosing different sizes of prey according to an optimal foraging strategy. For Redshank to optimise pecking rate, there would have to be a cost associated with pecking for prey. Speakman (1984) found that the energy expended by Redshank whilst pecking and probing was 1.9 and 2.0 times BMR respectively, whilst searching behaviour (i.e. walking at a speed of 30m/s) incurred a cost of only 1.7 times BMR.

In 1994/95 when *Corophium* densities were low, pecking rate decreased with increasing cumulative M_{maint} and cumulative air temperature, as well as with increasing air temperature whilst feeding. During this year, the frequency of cues from *Corophium* would have been much less than during the previous winter and thus, Redshank may have had to maximise pecking rate throughout the season in order to achieve the high rate of food intake. Hence, there was less scope within the foraging capabilities of Redshank at low prey densities to maintain a high rate of prey intake when prey availability was further reduced by cold temperatures. So, as conditions became colder and more energy demanding, the number of surface cues decreased. Since Redshank were pecking at the majority of cues encountered, pecking rate consequently went down. Hence at low prey densities during 1994/95, pecking rate was more reliant on ambient conditions whilst foraging, in contrast to the previous winter when higher prey densities allowed a wider scope of foraging responses to achieve a high rate of food intake.

Intake of large worms

The increase in the number of worms taken in 1994/95 may have been due to an increase in densitiy of worms (Goss-Custard, 1977a). Indeed densities of the most common large polychaete worm on Seal Sands *Nereis diversicolor*, did increase between autumn 1993 and autumn 1994 in 8 out of 10 cores taken from Scalloped Mud, with the maximum density increasing from $2288m^{-2}$ in 1993 to $4078m^{-2}$ in 1994, as shown in Figure 9 (data taken from Evans *et al.*, 1996). Despite high densities of *Nereis,* Goss-Custard (1977a&c) suggested that Redshank increase their intake of worms only when absolute densities of *Corophium* are low. It is unlikely that the low intake of worms in 1993/94 was the result of densities of *Nereis* being too low to support a sufficient intake, since Goss-Custard (1977a) recorded individual intake rates of 1-4 worms per minute (20-80 times greater than at Seal Sands in 1993/94) at sites where *Nereis* density exceeded $200m^{-2}$ and *Corophium* was absent. On the Ythan Estuary where the *Corophium* density was comparable to that on Seal Sands in 1993/94 and *Nereis* density was up to around $1000m^{-2}$, worm intake rate was around 0.2 per minute (Goss-Custard, 1970), only 4 times that at Seal Sands in 1993/94. Therefore, the increased intake of worms in 1994/95 appears to be a result of reduced *Corophium* density, rather than an

Figure 9: Densities of *Nereis diversicolor* at sampling stations on Scalloped Mud, Teesmouth.



increase in worm density which might also have explained an increase in worm ingestion rate (Goss-Custard, 1977c).

The findings during 1993/94 confirm Goss-Custard's (1969) suggestion that Redshank feed more on worms during low temperatures in response to a higher energy demand. The apparent negative correlation in 1994/95 between worm intake rate on Seal Sands and M_{maint} suggested that worm availability was limiting in this winter during periods of high energy demand. However, there was no correlation in either winter between worm intake and mean air temperature, minimum air temperature, mean windspeed or maximum windspeed on the day of feeding. There was, however, an apparent positive correlation in 1994/95 between the mean number of worms taken per bird and the mean air temperature on the day before (Spearman rank correlation $r_s = 0.513$ $P=0.061$). The significant increase in worm intake rate throughout the winter of 1994/95 may have been a response to the depletion of other prey such as *Corophium* and *Hydrobia,* which were less abundant than *Nereis* at the start of the winter.

Costs associated with feeding on large worms?

Goss-Custard (1977a) noted that Redshank feeding predominantly on *Corophium* could greatly increase their energy intake rate by taking more larger, energetically profitable prey such as *Nereis* which they appeared to ignore, even at high densities. The present study found that Redshank fed on large worms only during periods of high energy demand or when *Corophium* was relatively scarce (see also Goss-Custard, 1969, 1977a,b&c). These findings would suggest that feeding on worms is more costly than feeding on small prey items. Certainly, the handling time associated with large worms is much greater than with small prey which are swallowed almost immediately. During the present study, handling time for worms varied between 2 and 31 seconds. However, despite the lower rate of intake of worms, Goss-Custard (1977a) argued that the energy obtained from feeding on worms far out-weighed the energetic costs associated with doing so.

An alternative explanation is that feeding on worms requires the head of the bird to be lowered for longer and may reduce the level of vigilance towards potential predators. Alternatively or additionally, it may be that worms like *Nereis* taste unpleasant to Redshank which therefore avoid them unless the need for rapid intake of energy is great.

To feed or not feed

Goss-Custard (1969) suggested that Redshank would have to feed almost 'round the clock' to fulfil their energy requirements during winter. However, the present study found that Redshank at Seal Sands fed for shorter times during more energetically demanding periods. It would appear that the costs of M_{maint} associated with foraging on exposed mudflats may exceed after a certain time the energy to be gained from further intake of food, though no direct proof is available.

The relationship between time spent foraging during daylight hours and M_{maint} was identical in both 1993/94 and 1994/95, despite totally different feeding conditions between winters. A similar relationship in both winters would exist only if the energy gained from a particular time spent foraging was the same. It would appear then that by increasing their preference for worms in 1994/95 they were able to equal the energy intake of 1993/94 over the same time period. It seems therefore, that energy accrued from taking more worms in 1994/95 was sufficient to compensate for the loss in energy intake from smaller prey.

Summary

Redshank maximise the numbers of prey taken per minute (Goss-Custard, 1977b, Speakman, 1983) but do not maximise the rate of energy intake by preferring *Corophium* to the energetically more profitable *Nereis* (Goss-Custard, 1977a; Speakman 1984). My study has shown that they do not necessarily achieve a maximum rate of prey intake by maintaining a maximal rate of foraging. At high prey densities they had the scope to increase foraging rate to maintain maximum prey intake even when conditions reduced prey availability. When densities of their preferred prey, *Corophium,* were low there was less scope for Redshank to increase foraging rate to maintain a maximum prey intake. Hence, at low densities of *Corophium*, energy intake was supplemented by an increased intake of larger worms.